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PART II: ZOOLOGY

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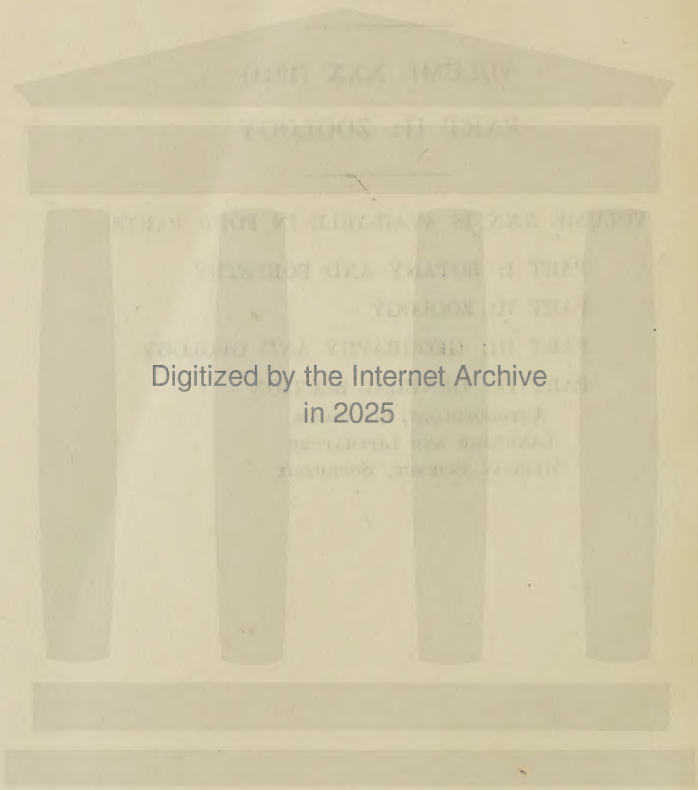

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PAPERS OF THE MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

EDITORS
EUGENE S. McCARTNEY
HENRY VAN DER SCHALIE

VOLUME XXX (1944)
PART II: ZOOLOGY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."
— SENECA, *Naturales Quaestiones*

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ZOOLOGY

GROWTH POTENTIAL OF THE NORTHERN PIKE (*ESOX LUCIUS*)*

WILLIAM F. CARBINE

IT HAS long been known that most fishes have an indeterminate type of growth, but it has only recently been appreciated that their potential rate of increase is vastly greater than their average growth in nature. Since fishes are also notably subject to dwarfing under conditions of overpopulation, extreme competition, and restricted space, it follows that the variation of size at a given age may be enormous. It is also known that a reduced growth in early life does not destroy the growth potential, for when placed under favorable conditions the dwarfed fish may grow at an unusually rapid rate. These phenomena have been determined chiefly through studies using the scale method of estimating age, but may be more directly and conclusively investigated by experiments. The present paper reports data relating to the growth of the northern pike obtained during the course of experiments conducted from 1937 to 1939. The results bear on each of the growth tendencies mentioned above.

These experiments were undertaken by the Institute for Fisheries Research of the Michigan Department of Conservation to obtain information on the possibility of artificially propagating northern pike. The data on the fish cultural problem will be reported elsewhere. The work was done at the Drayton Plains Hatchery, with the effective coöperation of A. T. Stewart, then District Fisheries Supervisor, and his staff. Thanks are also due to Dr. Albert S. Hazzard, Director of the Institute for Fisheries Research, for assistance in planning the work. I should like to express my appreciation to Dr. Carl L. Hubbs for aid in the analysis of the data and for suggestions and help in the preparation of this report.

The northern pike used in this experiment were hatched from eggs taken on April 7 and 8, 1937, at Walled Lake, Oakland County.

* Contribution from the Institute for Fisheries Research of the Michigan Department of Conservation.

On May 3 about 150,000 fry were stocked in the Ortonville Rearing Pond, which has an area of nearly three acres, an average depth of two and one-half feet, and a maximum depth of eight feet. Food for the growing pike was furnished by the introduction of 6,200 small minnows on June 2. On June 16 the pond was stocked with 30,000 largemouth-bass fry, and some of these were probably eaten by the northern pike. Sometime during the spring, probably during a period of heavy rainfall in early June, large numbers of fish, of nineteen species, gained access to the pond, and doubtless contributed to the nourishment of the pike. All the fish thus accidentally introduced, with the exception of 850 yearling bluegills, were young of the year. The yearling bluegills spawned successfully in the pond and produced a large number of young, which further augmented the already abundant food supply. The known source of these extraneous fish, along with other circumstances, makes it virtually certain that no pike were included.

Samples of the pike, seined on June 25, July 14, and August 17, were preserved to determine the length and weight. Of about 100 netted on the first date a random series of 40 was preserved. All the fish that could be seined on the other dates, 21 on July 14 and 12 on August 17, were kept (the soft bottom and the dense growth of plants made collecting difficult). When the pond was drained on October 14, 362 pike were recovered, along with many small minnows and bluegills. All these fish were individually weighed and measured.

A tremendous spread in length developed early in the growing season (Table I; Figs. 1–2; Pl. I). The pike in the June 25 sample ranged from 50 to 135 mm.; those in the July 14 series, from 62 to 222 mm.; those in the August 17 sample, from 79 to 263 mm. It is possible that the largest and smallest individuals in the pond on these dates escaped capture. The 362 fish remaining on October 14 had the unprecedented size range of 83 to 446 mm. (Pl. II), with the average at 207.2 mm. The great divergence in size obviously increased as the summer advanced. Many of the pike grew very rapidly and quite variably; others grew little and formed a very compact-sized group (Fig. 1).

The survival and growth of these pike in the Ortonville Pond followed the pattern of other highly predaceous fishes in pond culture. A few of the fish get a better start and grow to large and

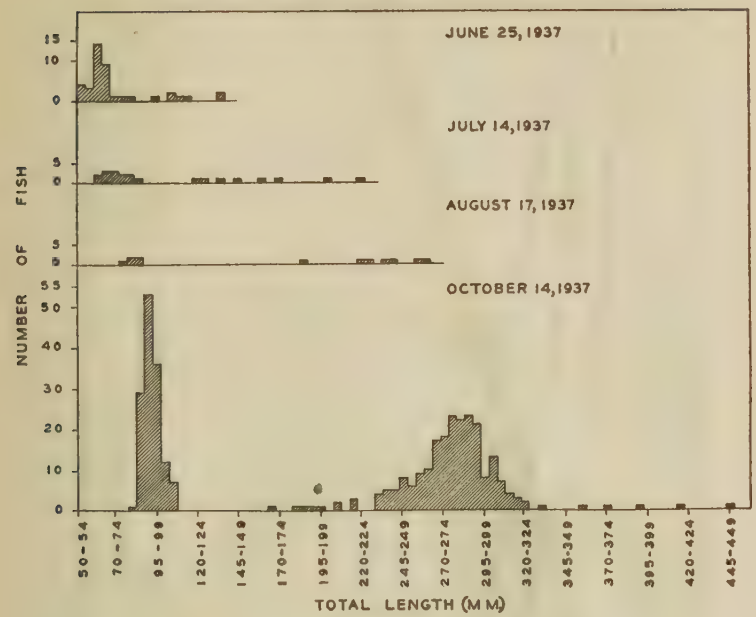

Fig. 1. Histogram showing the growth of the northern pike in the Ortonville Rearing Pond

variable sizes. Others, with a poorer start, find the competition so severe that they remain small and uniform in length. Cooper's study (1937) of pond-cultured largemouth bass illustrates these relations.

The largest fish taken on October 14 had grown at an average rate of 2.6 mm. (0.1 inch) per day. The largest fish at each collection date during the summer were all growing at a rate of more than 2.0 mm. per day, and the largest fish taken on July 14 was growing at a slightly faster rate (2.7 mm. per day) than the largest specimen taken on October 14 (Table I). Other workers (Embody, 1915; Webster, 1929; Rawson, 1932; Van Engel, 1940; Elson, 1941) have found that the northern pike and the muskellunge, a very close relative of the northern pike, are capable of exceedingly rapid growth. During part of the first season pike in nature grow as much as 3.3 mm. per day (Carbine, 1942). The only comparable rate of

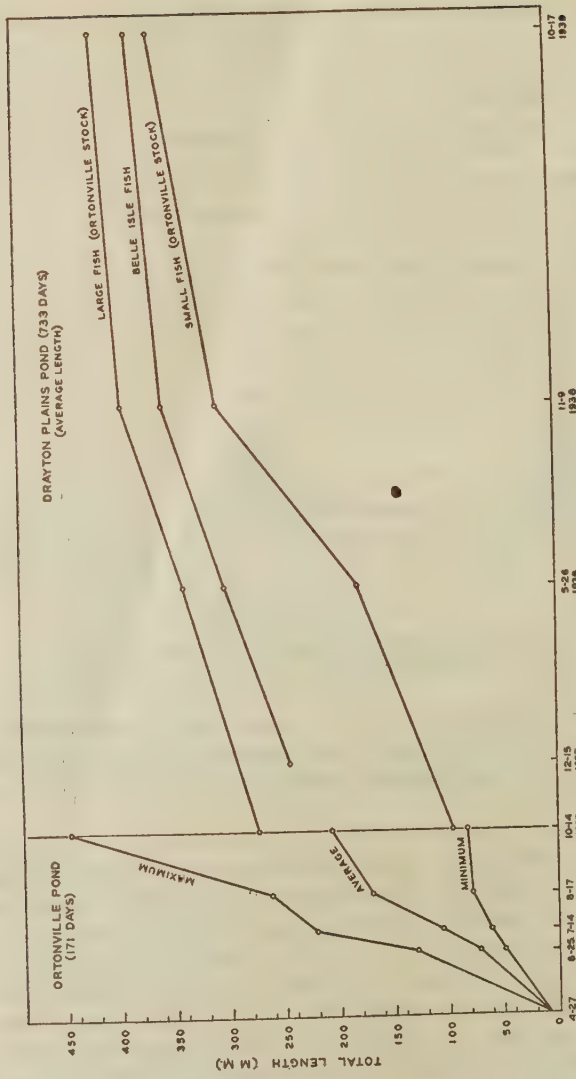

FIG. 2. Growth in length of the northern pike in rearing ponds at Ortonville and Drayton Plains

TABLE I

GROWTH OF THE NORTHERN PIKE IN THE ORTONVILLE POND FROM THE TIME OF HATCHING ON APRIL 27 UNTIL OCTOBER 14, 1937

Sampling date	Number of fish in sample	Age (days)	Total length (mm.)		Growth per day (mm.) *		Weight (grams)		Growth per day (grams)	
			Range	(Av.)	Range	(Av.)	Range	(Av.)	Range	(Av.)
June 25	40	60	50–135	(72.6)	0.7–2.1	(1.1)	–13	...	–0.22	...
July 14	21	79	62–222	(107.0)	0.7–2.7	(1.2)	1–78	(13.4)	0.01–0.99	(0.17)
Aug. 17	12	113	79–263	(171.0)	0.6–2.2	(1.4)	2–102	(46.7)	0.02–0.90	(0.41)
Oct. 14	362	171	83–446	(207.2)	0.4–2.6	(1.2)	2–460	(72.1)	0.01–2.69	(0.42)

* Northern pike are approximately 9 mm. long when hatched.

early growth per day which has been published is for the longnose gar, *Lepisosteus osseus* (Hubbs, 1921).

The diversity of growth in weight of the northern pike in the Ortonville Pond was even more striking (Table I; Fig. 3). On October 14 the smallest specimen weighed only 2 grams; the largest one, 460 grams (just over a pound). The 362 northern pike remaining on October 14 had grown an average of 0.42 gram in weight per day during the 171 days since hatching. The largest fish (460 grams) grew at the rate of 2.69 grams per day during this same period.

The extremely rapid growth of some of the pike in the Ortonville Pond is an example of the great growth potential possessed by fishes. The large food supply, warm temperature, and other conditions were obviously conducive to exceptionally rapid growth. Why, then, did some of the fish become stunted in the same pond, to produce the striking divergence in size? Several reasons come to mind.

It is possible that the small fish were diseased, though the evidence available does not favor this explanation. They were obviously emaciated, and all but 6 of the 140 died within five days after the removal of the fish from the Ortonville Pond to the Drayton Plains Hatchery, whereas none of the larger fish, treated in the same way, died during this period. Examination of those that died by Lowell A. Woodbury disclosed no external or internal parasites that could be regarded as responsible for the mortality. It is also possible, though inherently improbable, that the dwarfed fish had never learned to eat. Another theoretical possibility, that the dwarfs failed to grow because of genetic factors, is negated by the rapid growth made during the next season (p. 215). Overcrowding and the space factor may have contributed to the dwarfing of some of the pike in the pond, but such an explanation would be inconsistent with the very rapid growth of other pike in the same pond.

The most plausible explanation for the great diversity in size of the pike in the Ortonville Pond is that some of the fish obtained an advantage in feeding that was maintained through the season, whereas others lived under conditions that were unfavorable. An early start, due to hatching a day earlier or to earlier assumption of predation, may have given certain fish an initial advantage. Some may have taken up a habitat where food conditions were excellent, whereas others may have become established, either by random choice

or because other places were preëmpted, in sites where there was little food. In support of this view evidence may be cited that the young of the northern pike and the muskellunge do occupy definite home ranges of limited extent. While conducting another northern-pike experiment at Drayton Plains Hatchery in 1939 I learned that young pike could be found throughout the summer in definite spots about the pond. Similarly, Elson (1941) discovered that young muskellunge nearly always frequented certain well-defined areas. According to him, the young muskellunge do not range widely in search of food, but wait for the food organisms to come to them. He also noted that in trapping fingerlings one setting of a net would take two or more individuals, but several days intervened between the catches. He likewise stated that a lead of forty or fifty feet in length was no more effective on traps than a lead half that length. These observations suggest that the foraging range of the muskellunge is limited, and this evidence presumably applies also to the closely related northern pike. An early fixation of the feeding ranges, some favorable and others unfavorable, might well lead to differential growth.

The presence of the other nineteen species of fish in the pond brought about severe competition for food. Although an abundance of small fish was present, perhaps the largemouth bass and the perch were more adept at catching small fish than the small northern pike were. In an experiment to test the relationship between muskellunge fry and the fry of other species Elson (1941) placed muskellunge fry and largemouth-bass fry in the same container. Until the end of July they showed no inclination to molest each other, but competition for food was keen. The largemouth-bass fry were much more adept at capturing small minnows than the muskellunge were.

In discussing the feeding habits of the muskellunge MacKay and Werner (1934 : 315) stated: "Due to this habit of poising over its prey, the maskinonge often loses its victim, since the minnow fry are usually quite active and either swim away in the meantime or have started to swim away when the lunge strike, causing the latter to miss or obtain an insecure hold. Furthermore, the lateral body movements of the swimming minnow make it difficult for the maskinonge to strike accurately." The habits of the northern pike are very similar to those of the muskellunge, and it is believed that these observations made on the muskellunge apply to the northern pike.

It is therefore probable that the small northern pike in the Ortonville Pond were so weak and emaciated that they were not strong enough to catch minnows and were forced to subsist on inadequate food.

Further data on the growth of the northern pike were obtained at the Drayton Plains Hatchery, where the 6 survivors of the 140 small fish and 103 of the large fish that were taken in the draining of the Ortonville Pond on October 14, 1937, were kept in a pond until October 17, 1939. On December 15, 1937, 51 northern pike that were received from the Belle Isle Aquarium in Detroit were placed in the same pond with the other northern pike. The three series of pike were marked for future identification by clipping different fins for each lot. During the course of the experiment 65,295 minnows and perch were placed in the pond as food for the pike. Adult bluegills, which were also introduced, spawned successfully in the pond and produced an additional source of food. The pond was partly drained on May 26 and November 9, 1938, on which dates all the pike were counted and each lot was weighed as a unit, but individual weights and measurements of length were taken on only a random sample. All the pike were individually weighed and measured on October 17, 1939, when the pond was completely drained.

The tremendous growth made by some of the northern pike in the Ortonville Pond was not maintained throughout their retention at the Drayton Plains Hatchery (Table II; Figs. 2–5). The average growth increments in the rearing pond at the Drayton Plains Hatchery were as follows: 63.1 mm. from October 14, 1937, to May 26, 1938; 58.2 mm. from May 26 to November 9, 1938; 121.25 mm. for the first year; and only 26.3 mm. for the second year in the pond, from November 9, 1938, to October 17, 1939. These fish, therefore, made excellent growth during their first winter and first summer in the Drayton Plains Hatchery, but the increase in growth during the second full year was only 21.7 per cent of that of the first year. The marked decrease in the growth rate of the pike during their third year of life in a rearing pond caused them to be smaller than average at that age and made an unusually abrupt depression of the growth curve for the third year. By the end of their third summer, on October 17, 1939, the three groups in the Drayton Plains Hatchery ranged in average length from 14.3 to 16.4 inches, whereas in natural waters in Michigan northern pike usually reach the legal length of

TABLE II

GROWTH OF THE NORTHERN PIKE IN POND NO. 3 AT THE DRAYTON PLAINS HATCHERY BETWEEN OCTOBER 14, 1937, AND OCTOBER 17, 1939

Sampling dates *	Total length (mm.)		Increment † of average length (mm.)	Pct. increment of average length	Average weight (grams)	Increment of average weight (grams)	Pct. increment of average weight	Average growth per day	
	Range	(Av.)						Mm.	Grams
Small fish (Ortonville stock)									
Oct. 14, 1937	87–109	(95.6)	86.6	91	4.1	4.1	100	0.51	0.02
May 26, 1938	160–197	(179.7)	84.1	47	31.6	27.5	87	0.38	0.12
Nov. 9, 1938	254–336	(307.2)	127.5	42	145.2	113.6	78	0.76	0.68
Oct. 17, 1939	356–373	(363.8)	56.6	16	230.0	84.8	37	0.17	0.25
Large fish (Ortonville stock)									
Oct. 14, 1937	195–371	(274.1)	265.1	97	101.3	101.3	100	1.55	0.59
May 26, 1938	297–385	(339.1)	65.0	19	227.5	126.2	55	0.29	0.56
Nov. 9, 1938	347–535	(394.0)	54.9	14	319.2	91.7	29	0.33	0.49
Oct. 17, 1939	260–652‡	(417.1)	23.1	6	361.7	42.5	12	0.07	0.12
Belle Isle fish									
Dec. 15, 1937	209–305	(245.2)	236.2	96	61.9	61.9	100	...	...
May 26, 1938	272–326	(301.6)	56.4	19	168.4	106.5	63	0.35	0.66
Nov. 9, 1938	324–396	(356.5)	54.9	15	234.0	65.6	28	0.33	0.39
Oct. 17, 1939	357–420	(384.3)	27.8	7	267.3	33.3	12	0.08	0.10

* A random sample of fish taken on May 26 and November 9, 1938, was measured; all fish were weighed and counted.
† The eggs hatched on April 27, 1937, at which time the fry were approximately 9 mm. long.
‡ This fish was probably missed on May 26 and November 9, when only a random sample of fish was measured.

14 inches early in their second summer, according to Dr. W. C. Beckman (unpublished report, Institute for Fisheries Research). As shown in Figure 4, the small fish remained smaller than average and the large fish larger than the mean until the end of the second summer, when the growth of both groups leveled off, to fall far below the average for the species during the third year. The basis of comparison, the curve of growth in natural waters, is taken from Van Engel's extensive data (1940) for the pike of Wisconsin, which grow at about the same rate as the pike in Michigan, as determined by Beckman. Because the time at which the annulus forms on the scales of Wisconsin fishes has not been determined it has been assumed (Fig. 4) that the time of the formation of the annulus in Michigan is the same as that for Wisconsin. In Michigan Beckman (1943) determined that the formation of the annulus may be expected to be completed by the first of June (average for the entire state), except in unusually cold years.

The depressed growth of the adult pike in the rearing pond during the third year of life may be attributed to the space factor (the Drayton Plains Hatchery was stocked at the rate of 320 northern pike per acre). It is thought that, despite the presence of large quantities of food, northern pike will grow very little in rearing ponds after they have attained a certain size. This species appears to require large bodies of water in order to reach large size.

The growth of the small and the large pike at the Drayton Plains Hatchery furnished an experimental demonstration of the principle of "growth compensation." This term was proposed by Gilbert (1914), who found that salmon (*Oncorhynchus nerka*) which were large at the end of the second year of life grew in succeeding years more slowly on the average than the fish that were small at the end of the second year. Eventually all individuals reached a nearly uniform length at maturity. Van Oosten (1929) determined that the law of growth compensation holds for the lake herring (*Leucichthys artedi*), but although the lengths of the small fish and the large fish became more uniform in each succeeding year of life (the smallest yearlings became the fastest-growing fish and the largest yearlings the slowest-growing fish), the length of the smallest fish did not quite come to equal that of the large fish in later years. Hubbs (1921; 1921a) and Hile (1936) also found that fish which grew more slowly than usual in early life compensated for the de-

ficiency by growing faster in later life. There is a large body of other data to indicate that the growth potential of animals is not readily destroyed by a stunting of the early growth.

It is obvious that the small fish grew faster in the Drayton Plains Hatchery than the medium- and large-sized fish did (Figs. 2–5), but, when the pond was drained on October 17, 1939, the small fish had almost caught up with the medium-sized ones, whereas the growth in length of the medium-sized ones paralleled that of the large fish. The rapid growth that was made by the small pike, particularly during their second summer, is a striking example of the great growth potential possessed by the northern pike. Although the differences in the lengths of the three groups diminished during each of the two years, the small fish never quite attained the size of the large fish (Figs. 4–5). The increments in length of each of the three groups of northern pike during each growth period between sampling dates shows that the small fish were the fastest-growing fish and the large fish were the slowest-growing (Table III). This table also shows that these small northern pike were not "genetic runts." Although the small fish got off to a bad start in their first summer, when they were given the proper conditions they were able during the next two years to overcome very largely the effects of the unfavorable conditions to which they were subjected in their first summer of life.

SUMMARY

A tremendous spread in length developed early in the season in northern pike reared in hatchery ponds, and this great divergence increased as the summer advanced. Many of the pike grew rapidly and quite variably, but others grew very little and formed a compact-sized group. The growth of the northern pike in rearing ponds follows the pattern of other highly predaceous fishes in pond culture.

The extremely rapid growth of some of the northern pike in rearing ponds is an example of the great growth potential possessed by fishes. The largest fish at the end of the first summer had grown at an average rate of 2.6 mm. and 2.69 grams per day.

The tremendous growth made by some of the northern pike during their first summer was not maintained throughout their retention in rearing ponds for two additional years. It is believed that northern pike will grow very little in such ponds after having attained a certain size.

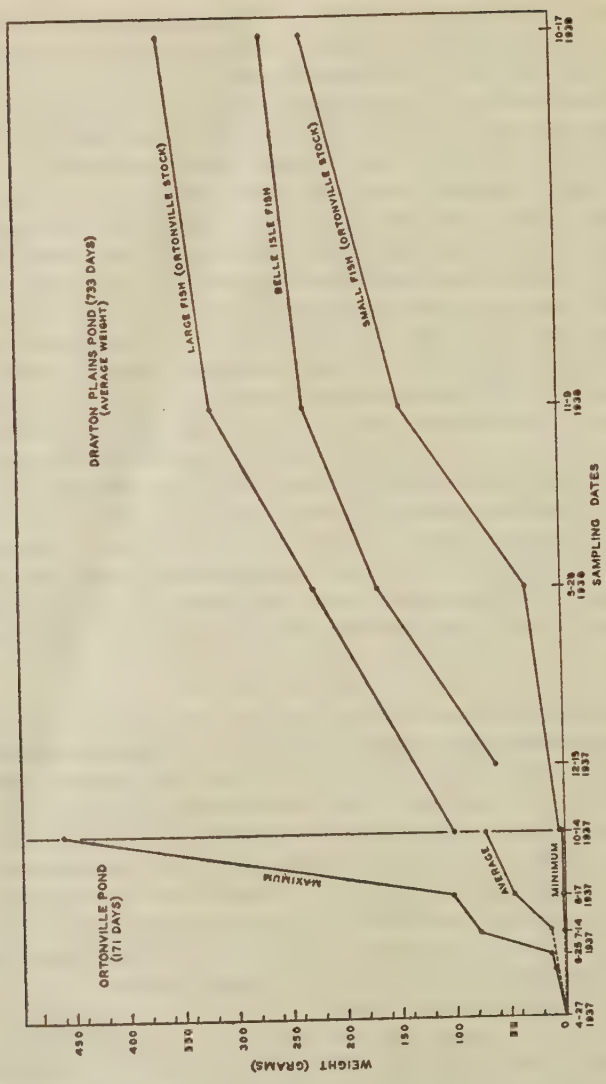

FIG. 3. Growth in weight of the northern pike in rearing ponds at Ortonville and Drayton Plains

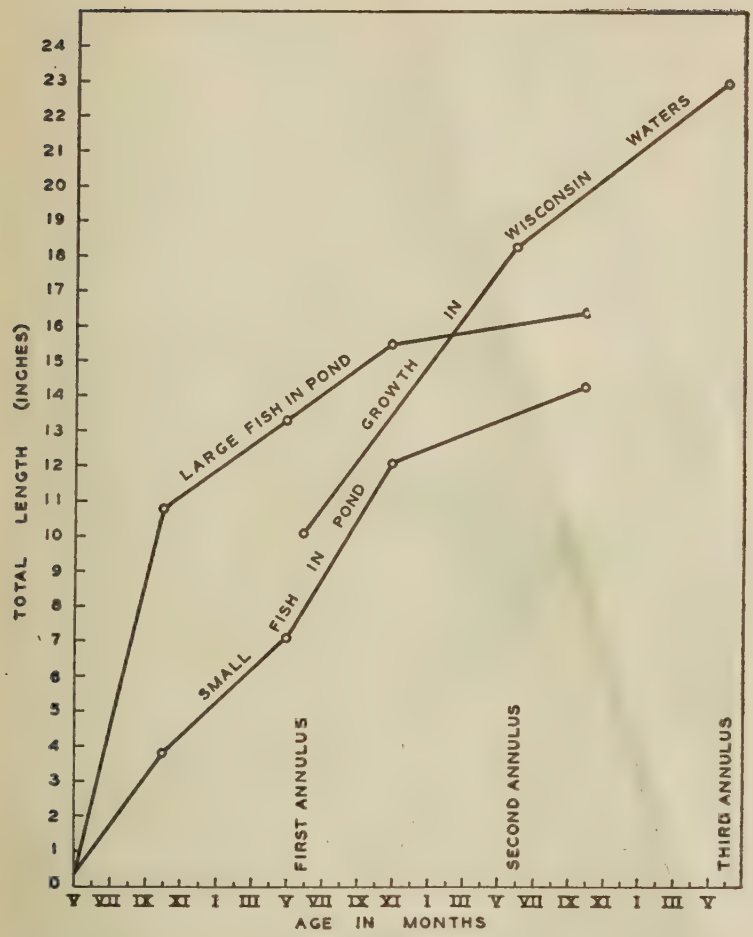

FIG. 4. Growth of small and large northern pike in rearing ponds and the average calculated growth of the species in natural waters

The growth of the northern pike in rearing ponds furnished an experimental demonstration of the principle of growth compensation. The smallest fish at the end of the first year became the fastest-growing fish in succeeding years, and the largest became the

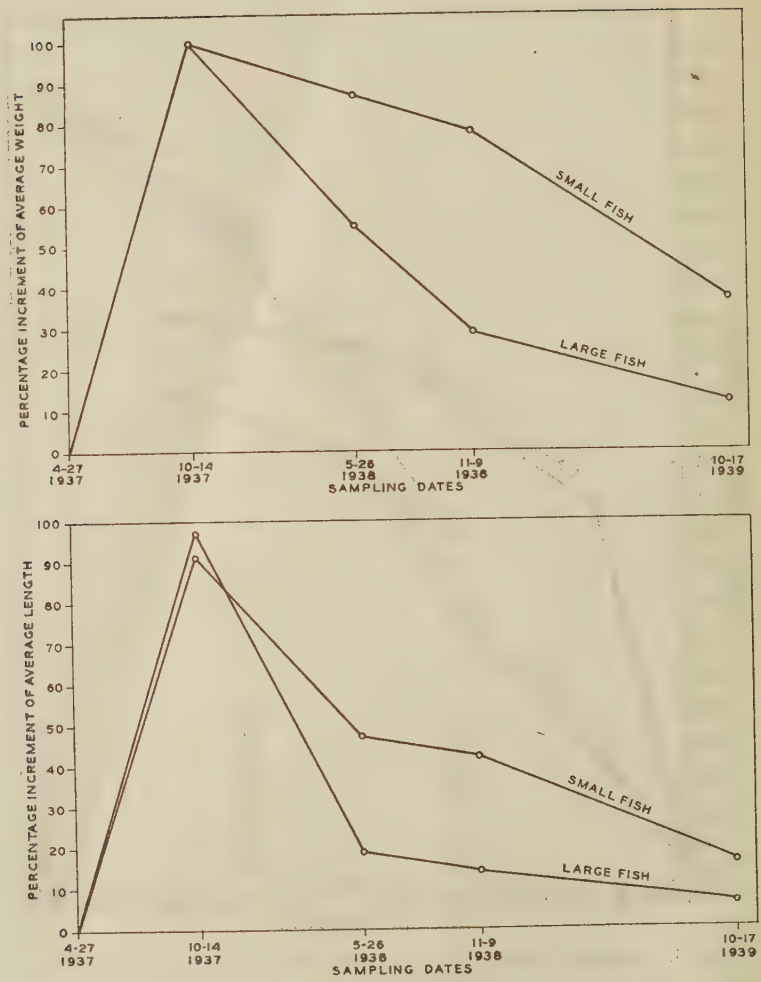

FIG. 5. Percentage increments of the average weight and average length of small and large northern pike in rearing ponds at Ortonville and Drayton Plains

TABLE III

THE AVERAGE INCREMENT OF LENGTH AND WEIGHT AT EACH COLLECTION DATE FOR THE THREE SIZE GROUPS OF NORTHERN PIKE REARED AT THE DRAYTON PLAINS HATCHERY

Size group	Length of fish at hatching (mm.)	Average increment in length (mm.)				Average total length Oct. 17, 1939	
		Oct. 14, 1937	May 26, 1938	Nov. 9, 1938	Oct. 17, 1939	Mm.	Inches
Small fish	9.0	86.6	84.1	127.5	56.6	363.8	14.3
Belle Isle fish	9.0	236.2*	56.4	54.9	27.8	384.3	15.1
Large fish	9.0	265.1	65.0	54.9	23.1	417.1	16.4
Size group		Average increment in weight (grams)				Average weight Oct. 17, 1939	
		Oct. 14, 1937	May 26, 1938	Nov. 9, 1938	Oct. 17, 1939	Grams	Ounces
Small fish		4.1	27.5	113.6	84.8	230.0	8.1
Belle Isle fish		61.9*	106.5	65.6	33.3	267.3	9.4
Large fish		101.3	126.2	91.7	42.5	361.7	12.8

* The average weight and average length of the Belle Isle fish are for December 15, 1937, the date that these fish were placed in the rearing pond.

slowest-growing. The rapid growth that is made by these small fish is another striking example of the growth potential of the northern pike.

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Group photograph of northern pike collected at the Ortonville Rearing Pond on June 25, 1937. These fish range in size from 50 to 135 mm.

Group photograph of northern pike collected at the Ortonville Rearing Pond on October 14, 1937. These fish range in size from 83 to 446 mm.

THE GREEN HALICTINE BEES OF THE GENERA *AGAPOSTEMON*, *AUGOCHLORA*, *AUGOCHLORELLA*, AND *AUGOCHLOROPSIS* (HYMENOPTERA: APOIDEA) IN MICHIGAN, WITH KEYS AND DISTRIBUTION

ROBERT R. DREISBACH

THE bees of the genera *Agapostemon*, *Augochlora*, *Augochlorella*, and *Augochloropsis* are easily identified by their metallic-green or blue-green color. Except in the genus *Agapostemon* both the males and the females have the head, thorax, and abdomen concolorous. In the genus *Agapostemon* the females, with few exceptions, are colored likewise, whereas in the males and a few females the head and thorax are in some shade of green, but the abdomen is marked by yellow and black crossbands. These bees are of about the same color as the Chrysididae or cuckoo wasps, from which they may be separated by the presence of only three or four visible abdominal tergites, by the concave ventral segments, by the concave front below the antennae, and by the absence of branched hairs in Chrysididae. As usual in the Hymenoptera, the males have seven abdominal tergites and thirteen antennal segments; the females have only six and twelve, respectively.

Miss Grace Sandhouse has monographed this group in two papers (1, 2). Her keys for the genus *Agapostemon* can be used for the Michigan species, although at present only four of the eight species and one variety of the genus have been collected in this state. The one variety and three of the other four species may be found in Michigan at some later date. Only one species of the genus *Augochlora* has been recorded from Michigan, and no other is likely to be found. Of the four species of *Augochlorella* one is very common in Michigan, and there is a doubtful record of a second, which most certainly will be collected here, since it is recorded from the neighboring states of Illinois and Indiana.

The key for the genus Augochloropsis as given by Miss Sandhouse contains two species for the United States. There are four species and a variety in the writer's collection, and apparently there are at least five species and three varieties in the United States. *Augochloropsis cuprea* (Sm.) has a strong fringe of hairs on the first and second abdominal tergites, whereas *A. viridula* Sm. has only a weak fringe laterally, which is almost wholly absent in the center. She noticed this, but thought of the hairs as having been worn off and mentioned that, where the hairs have been lost, there is a row of tiny punctures. These two species have other and just as great differences that clearly distinguish them. They were considered one species by Miss Sandhouse. There is a third species of this genus which should be found in Michigan since it has been collected in South Dakota. This species is *A. humeralis* (Patton), the *A. caerulea* (Ash.) of Miss Sandhouse. Patton's name should be used since it antedates the other and is not preoccupied.

The writer wishes to thank Dr. P. H. Timberlake, of the Citrus Experiment Station, Riverdale, California, for his determination and checking of species, and also for his suggestions and help in the synonymy and keys in the genus *Augochloropsis*.

KEY FOR THE SEPARATION OF THE GENERA

1. Posterior tibiae about equal to length of tarsal joints; female: hind tibiae with knee plate absent, and inner calcar pectinate, with three to five very broad spatulate teeth; head, thorax, and abdomen concolorous with some shade of bright green, except in three species and a variety in which abdomen is black or brown; legs brown or yellowish brown; male: head and thorax blue green, abdomen transversely banded with black and yellow; posterior femur usually much thickened and distinctly thicker than trochanter, toothed below near apex; legs yellow, variously marked with black ..... *Agapostemon*

1. Posterior tibiae about equal to first tarsal joint only; female: hind tibiae with knee plate present, inner calcar pectinate or serrulate, pectinations narrow, pointed; head, thorax, and abdomen concolorous; some part of legs green, the amount depending upon the species; male: head, thorax, and abdomen concolorous with some shade of green; posterior femur neither thickened nor toothed; legs green and black, with tarsi in some specimens yellow 2

2. Pubescence uniformly of one kind and directed posteriorly; tegula large and greenish; posterior tibiae of female with inner calcar with narrow acute pectinations; carinae on lateral margins of propodeum extending almost to dorsal surface; male: tergites beyond third partially retracted within the third; fourth sternite concealed under the third and

with long posterior lateral processes; margin of fifth emarginate; posterior margin of fourth with median projection; labrum with median basal groove ..... *Augochloropsis*

2. Pubescence consisting of long and short hairs, the long hairs pointing posteriorly and the short ones laterally; carinae on lateral margins of propodeum extending less than halfway to dorsal surface; posterior tibiae of female serrulate with many fine, short serrulations; tegula smaller, brown or testaceous; male: tergites beyond third not retracted within the third; fourth sternite not concealed under the third and without long posterior lateral processes; margin of fifth truncate, that of fourth either truncate or emarginate 3

3. Apex of radial cell slightly truncate, with appendiculation; head broad, ocellocular line longer than postocellar; first sternite of female with median carina or toothed, sixth with median polished area; posterior margin of fourth sternite of male truncate ..... *Augochlora*

3. Apex of radial cell acute without appendiculation; head narrow, ocellocular line equal to postocellar; first sternite of female without carina or tooth, and sixth without median polished area; posterior margin of fourth sternite of male emarginate ..... *Augochlorella*

KEY TO THE GENUS *AGAPOSTEMON*

(Based largely on the paper by Miss Sandhouse. Species marked with an asterisk have not yet been found in Michigan.)

1. Females, six abdominal tergites and twelve antennal joints 2
1. Males, seven abdominal tergites and thirteen antennal joints 8

2. Head, thorax, and abdomen concolorous 3
2. Head and thorax green, abdomen brown or black 6

3. Mesonotum of thorax with punctures of one size and nearly contiguous 4
3. Mesonotum of thorax with punctures of two sizes and not contiguous .. 5

4. Mesonotum more finely and uniformly punctured, space between punctures smooth; dorsal surface of propodeum with irregular carinae, appearance dull ..... *A. splendens* (Lepel.)
4. Mesonotum more coarsely punctured, space between punctures rough; dorsal surface of propodeum with regular longitudinal carinae, appearance shining ..... *A. radiatus* (Say)

5. Mesonotum with punctures separated by about their diameter; dorsal surface of propodeum irregularly carinate and usually with distinct triangular area; pubescence tinged with yellow; about 12 mm. in length ..... *A. texanus* Cress.
5. Mesonotum with punctures separated by about twice their diameter; dorsal surface of propodeum with regular longitudinal carinae; pubescence white, about 10 mm. in length ..... *A. angelicus* (Ckll.) *

6. Broad basal band of white hair on first abdominal tergite; apex of clypeus black and yellow; abdominal tergites brown or black but tinged with brown or blue-green apically; hair on posterior part of tergites white; wing veins honey yellow 7
6. Two patches of white hair only on lateral sides of first abdominal tergite; apex of clypeus black; abdominal tergites black, not tinged with blue

green apically; hair on posterior part of tergites black; wing veins light brown ..... *A. virescens* (Fab.)

7. Scape dark brown; apex of abdomen tinged with blue green; apical margin of clypeus black, yellow not extending upward in the middle *A. melliventris* var. *plurifasciatus* (Vachal.) *

7. Scape yellow; apex of abdomen brown; apical margin of clypeus yellow, yellow extending upward to form triangle ..... *A. melliventris* Cress.*

8. Dark bands on middle tergites about one third length of tergite; base of first tergite generally of brownish tint but never black; femur, tibia, tarsi yellowish except for brownish spot at apex of posterior femur and one at base of posterior tibia; posterior femur scarcely wider than trochanter, the tooth very weakly developed 9

8. Dark bands on middle tergites about one half length of tergite; base of first tergite black; femur, tibia, and tarsi yellowish, but more heavily marked with black; posterior femur very distinctly wider than trochanter, the tooth strongly developed; wings infumated 10

9. Dark bands on abdominal tergites not reaching lateral margins; scape entirely yellow, or with small brownish dot on upper side; trochanters of front and middle legs yellow, those of hind legs tinged with green. *A. melliventris* Cress.*

9. Dark bands on abdominal tergites reaching lateral margins; scape with upper side brown; trochanters of all legs green *A. melliventris* var. *plurifasciatus* (Vachal.) *

10. Apical abdominal tergites, laterally, strongly tinged with metallic blue green 11

10. Apical abdominal tergites dull black, without metallic tints 12

11. Dorsal surface of propodeum with distinct triangle in middle; front and middle trochanters black or black and yellow, if entirely black, then bases of femur are marked with black; posterior tibia always with long black mark on anterior surface, but posterior surface may or may not be similarly marked ..... *A. texanus* Cress.

11. Dorsal surface without distinct triangle in middle; all trochanters black, but without black on bases of femur; posterior surface of hind tibia with long black mark, but never with one on anterior surface *A. angelicus* Ckll.*

12. Posterior femur strongly swollen, its width distinctly more than one half its length 13

12. Posterior femur not so strongly swollen, its width distinctly less than one half its length ..... *A. splendens* (Lepel.)

13. Species about 9 mm. long; dorsal surface of propodeum with mainly longitudinal carinae, although there are some cross or irregular carinae; abdominal sternites more than half yellow; apical margins of fourth sternite with median green spot; front and middle trochanters and bases of corresponding femur yellow ..... *A. radiatus* (Say)

13. Species about 11 mm. long; dorsal surface with irregular carinae without any tendency to be longitudinal; abdominal sternites black; apical margin of fourth sternite without median green spot; all trochanters black, and bases of femur also marked with black *A. virescens* (Fab.)

KEY TO THE GENUS *AUGOCHLORELLA*

1. Sides of propodeum with vertical striations; color blue green to purplish tints; posterior vertical face of propodeum nearly smooth; legs lighter brown, especially posterior femur, which shows less of a metallic tint *A. neglectula* Ckll.

1. Sides of propodeum with striations crossing and forming large cells (reticulate); color bright green to coppery green; posterior vertical face of propodeum rougher, with faint indications of transverse striations; legs darker, especially the posterior femur, which shows a darker shade and more of a metallic tint ..... *A. striata* (Prov.)

KEY TO THE GENUS *AUGOCHLOROPSIS*

1. Pronotal carina with angles sharp and prominent; supraclypeal area uniformly convex and punctured; tergites of abdomen tessellate and dullish; sides of propodeum, above, closely reticulately punctured; sternites brown to yellowish, may be faint greenish tints on two and three ..... *A. humeralis* (Patton) *

1. Pronotal carina with the angles rounded and not so prominent; supraclypeal area flattened, shining, and sparsely punctured; tergites of abdomen scarcely or not at all tessellate and shining; sides of propodeum, above, closely but hardly reticulate-punctured; sternites two, three, and four greenish 2

2. Tergites one and two with dense fulvous apical fringe; abdominal tergites one and two rather densely and conspicuously punctured; tergites three and four with smooth broad apical edge with deep purple color *A. cuprea* (Sm.)

2. Tergites one and two with apical fringe all but absent, present as very sparse and short fringe laterally; tergites one and two with punctures finer and less conspicuous; tergites three and four with smooth broad apical edge of same color as remainder of tergite, namely, green *A. viridula* Sm.

The distributional records listed below are based on the collections at the University of Michigan and Michigan State College, and the private collection of the writer.

Of the eight species of these genera recorded for Michigan three have been taken in the Upper Peninsula and one other should be found there. All the species have been found in the Lower Peninsula. With the exception of *Augochloropsis viridula* Sm. and *Augochlorella neglectula* Ckll. the species seem to be reasonably common throughout their range.

ANNOTATED LIST OF SPECIES IN MICHIGAN

AGAPOSTEMON RADIATUS Say. — Dates of capture: May 23 to October 3. U. P.:[1] Gogebic. L. P.: Cheboygan, Leelanau, Benzie, Manistee, Lake, Osceola, Clare, Gladwin, Arenac, Mecosta, Isabella, Midland, Bay, Huron, Montcalm, Gratiot, Saginaw, Sanilac, Lapeer, Ingham, Oakland, Calhoun, Washtenaw, Wayne, Berrien, Branch.

AGAPOSTEMON SPLENDENS. — Dates of capture: June 3 to September 20. L. P.: Emmet, Cheboygan, Alcona, Manistee, Missaukee Roscommon, Lake, Clare, Arenac, Oceana, Isabella, Newaygo, Mecosta, Midland, Huron, Muskegon, Gratiot, Saginaw, Lapeer, Ingham, Oakland, Washtenaw, Berrien.

AGAPOSTEMON TEXANUS Cress. — Dates of capture: May 24 to September 13. L. P.: Alcona, Missaukee, Oceana, Midland, Lapeer, Oakland, Washtenaw, Wayne.

AGAPOSTEMON VIRESCENS Fabr. — Dates of capture: May 30 to September 20. L. P.: Cheboygan, Clare, Newaygo, Midland, Gratiot, Saginaw, Tuscola, Eaton, Livingston (George Reserve), Oakland, Calhoun, Washtenaw, Wayne, Hillsdale.

AUGOCHLORA PURA (Say). — Dates of capture, May 25 to August 27. U. P.: Ontonagon, Baraga, Gogebic, Dickinson, Alger, Mackinac. L. P.: Cheboygan, Charlevoix, Grand Traverse, Manistee, Mason, Mecosta, Midland, Huron, Lapeer, Ingham, Oakland, Van Buren, Washtenaw, Wayne.

AUGOCHLORELLA NEGLECTULA Ckll. (*A. aurata* (Sm.), comb. nov. of Miss Sandhouse). — L. P.: Elmdale, Michigan (Kent Co.?). This collection is given by E. S. G. Titus (3, p. 134) under the name *A. similis* Robt.

AUGOCHLORELLA STRIATA (Prov.). — Dates of capture: April 26 to September 3. U. P.: Marquette, Mackinac. L. P.: Emmet, Cheboygan, Antrim, Otsego, Montmorency, Benzie, Crawford, Missaukee, Roscommon, Ogemaw, Iosco, Mason, Lake, Clare, Gladwin, Arenac, Oceana, Newaygo, Mecosta, Isabella, Midland, Bay, Huron, Muskegon, Montcalm, Gratiot, Saginaw, Tuscola, Sanilac, Shiawassee, Genesee, Lapeer, Eaton, Livingston (George Reserve), Oakland, Kalamazoo, Washtenaw, Wayne, Berrien.

[1] U.P., Upper Peninsula; L.P., Lower Peninsula.

AUGOCHLOROPSIS CUPREA (Sm.). — Date of capture: Aug. 2, 1944. L. P.: Muskegon.

AUGOCHLOROPSIS VIRIDULA Sm. — Dates of capture: July 24 to August 9. L. P.: Oscoda, Lake, Livingston (George Reserve), Kalamazoo.

MIDLAND, MICHIGAN

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BILATERAL ASYMMETRY AND BILATERAL VARIATION IN FISHES *

CARL L. HUBBS AND LAURA C. HUBBS

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Introduction

ONE ordinarily sees in bilaterally symmetrical animals creatures composed of identical halves, each a mirror image of the other. Closer scrutiny, however, discloses some degree of asymmetry in many of the paired structures. The differences between the two sides usually involve the internal organs, but also affect certain superficial structures, as well as reactions and movements. Bilateral unlikenesses may be rare, common, unusual, or invariable. When the sides are different, the better development may occur on the left side or on the right side, or sometimes on the left and sometimes on the right, in any conceivable ratio. The differences between the sides may involve the presence or the absence of a structure, the size or the shape of paired elements, or the number of meristic parts. Asymmetries are known to characterize all stages of development, from the unfertilized egg to the dying adult.

Fishes, like all other vertebrates, exhibit such differences between the corresponding structures of the left and right sides. Many bilateral dissimilarities have been treated. The numerous scattered contributions are most adequately summarized in a book, *Das Rechts-Links-Problem im Tierreich und beim Menschen*, by Wilhelm Ludwig (1932). Most of the recorded asymmetries, however, have been inadequately described or unsatisfactorily explained.

The objects of this study are to present new data on the bilateral differences between the left and the right elements of paired structures of fishes; to integrate these findings with previously recorded information; to analyze new and old data by modern statistical methods; to contribute suggestions that may help to explain the observed differences; to give a general picture of the asymmetries; to discuss the bearing of these findings and interpretations on the question of right-handedness in man, and on problems in such fields of biology as general systematics and evolution; and

to offer suggestions for further researches on the bilateral asymmetries of fishes.

Particular attention is paid to the flatfishes (order Heterosomata), the most extremely asymmetrical of all vertebrates. Bilateral differences in external characters are emphasized. The major asymmetries in the digestive and circulatory systems are in general neglected, as they are well known and were extensively summarized, for vertebrates in general and for fishes, by Ludwig (1932 : 224–237, figs. 109–110). Similarly, only incidental consideration is given to asymmetries in the egg and in the embryo, and to bilateral differences in growth and movements. Numerical differences are the most thoroughly analyzed, according to methods that call for some explanation.

Statistical Methods

The chief attempt to develop a statistical method for the analysis of quantitative bilateral asymmetries appears to have been made by the German zoologist and biometrician Georg Duncker (1904), in a treatise entitled "Symmetrie und Asymmetrie bei bilateren Thieren." Duncker's statistical methods were reviewed and accepted by Ludwig (1932 : 4–8).

Duncker (1904 : 555) proposed an index of asymmetry, designated α, with the following formula:

$$\alpha = \frac{\Sigma(f') \cdot \Sigma(D') - \Sigma(f_{,}) \cdot \Sigma(D_{,})}{n[\Sigma(D') + \Sigma(D_{,})]},$$

in which the differences are all expressed in terms of right count minus left count, and

f' = frequencies of positive differences, without regard to amount of difference;

D' = positive differences ($f' \times \Delta$); for example, when the counts of parts are 13 on the right and 10 on the left, $f' = 1$ and $D' = 3$;

$f_{,}$ = frequencies of negative differences;

$D_{,}$ = negative differences; for example, counts of 10 on the right and 13 on the left give $f_{,} = 1$ and $D_{,} = 3$;

n = number of specimens. Symmetrical counts (as 10 left and 10 right) are included in n, but are otherwise disregarded in the formula.

It can be shown that the index of asymmetry has one of the

desirable features of the coefficient of correlation in that complete asymmetry is represented by an index of + 1 when the stronger development is on the right, and of − 1 when the left side is the better developed. Complete symmetry is indicated by 0.

The formula for α was derived by empirical trial. How sound it may be as a joint measure of the amount and direction of asymmetry we do not know. We have avoided the use of the formula because we see no way of estimating the standard error of the index and, more particularly, because it does not fit our purposes. It is true that Ludwig fixed an α value of about 0.05 as the threshold of significance, but apparently by unwarranted, arbitrary choice.

Our main objection to the use of Duncker's index is that it confuses two functions of asymmetry — amount and direction. When the proportion of asymmetry is low, the value of α will be low even though among the few asymmetrical individuals the rights may strongly predominate over the lefts, or vice versa. Thus, for a sample in which every one of the 100 variants out of 10,000 specimens has a higher count on the right side, $\alpha = 0.01$, though the significance of the direction of asymmetry — among the asymmetrical individuals, of course — is unquestionable. In a second series in which, out of a total of 100 specimens, 50 have the count greater on the right side and 40 have a higher number on the left, $\alpha = 0.1$ — a value far above Ludwig's limit of significance. For the first sample the value of α is one tenth as great as in the second series, yet the direction of asymmetry is much more definite and almost infinitely more significant.

We have separated the two functions of asymmetry. The *amount* of overall asymmetry is expressed as a percentage figure,

$$\frac{100\,(L + R)}{N},$$

in which L and R represent counts that are higher or development that is otherwise better (on some indicated basis) on the left and right sides, respectively, and N is the total number of specimens, symmetrical plus asymmetrical, in the sample. The values for N, L, and R are tabulated. Since we are only incidentally interested in the amount of asymmetry, we have not tried to determine the standard error of the percentage of asymmetry.

The *direction* of asymmetry in the portion of the sample having

different values on the two sides is expressed in the tables by the percentage of dextrality,

$$\frac{100\,R}{L+R},$$

in which L and R have values as indicated above. The reliability of observed differences between the sides is determined from the values for L and R by the now widely used χ^2 test, and the Yates correction is applied when the expected number (the median between the L and R values) is less than 25. The method is described in most textbooks of statistics, for instance, in Snedecor (1940: 168–171) and Simpson and Roe (1939: 296–300).

The probability (P) that the ratio of lefts and rights differs from one of equality, in other words, that the result could have been obtained by chance alone, is generally given. In the tables a percentage figure (100 P) is entered, indicating the probabilities in 100 that the results are due to chance. The 100 P values are expressed as whole numbers (chances in 100), or to tenths (1 to 9 chances in 1,000), or to hundredths, from 0.01 to 0.09 (1 to 9 chances in 10,000). The 100 P values of 0.00 indicate values of less than 0.005; that is, probabilities of less than 1 in 20,000 that the results are due to chance. Too strict reliance on these P values is unwarranted, for several statistical reasons, but, relatively speaking, they are valuable as an index of the reliability of the observed differences. The naïve faith of biologists in a definite threshold of reliability, at $P = 0.01$ or $P = 0.05$, is to be condemned and avoided. Much higher values afford some evidence of significance, to the degree of reliability indicated by the value of P.

The tables in textbooks give only a few corresponding values of χ^2 and P, but, since in the simple comparison of two figures or in "2×2 tables" χ^2 has one degree of freedom, and since χ at one degree of freedom equals t with an infinite degree of freedom, one needs merely to read off the P value corresponding to $\chi = t$, at 0 skewness, in the newer tables (Salvosa, 1930: tables, pp. 1–60; Carver, 1940: 1–61; Lowan, 1942). It needs be noticed that Salvosa's table, repeated by Carver, gives half of the area of the Type III curve, whereas the "W. P. A. table" (edited by Lowan) gives the whole area. To arrive at the P value the figures in either table are to be subtracted from 1, but the differences obtained from the use of Salvosa's table are to be multiplied by 2.

Dextrality and Sinistrality in Flatfishes

When one thinks of left-handedness and right-handedness in fishes, his thoughts are apt to turn first to the fishes of the order Heterosomata, in which, during the metamorphosis, one eye shifts to the top of the head, or, more commonly, to the opposite side, so that either the left or the right side comes to bear both of the eyes, leaving the other half of the body blind. During the transformation many asymmetries develop: to a greater or a lesser degree, depending on the genus and species, the anterior part of the skull becomes twisted; the muscular development is more or less weakened on the blind side; the teeth in many species become reduced in number or even totally lost on the eyed side; the color disappears from the blind side; and other inequalities appear. The general morphological nature of the asymmetry is well known (for discussion and references see Norman, 1934 : 10–22) and the adaptational advantage is obvious, but the reasons why some species lie on the left side, others on the right side, and still others on either side remain unexplained. The problem warrants new study.

The two species of the genus *Psettodes*, constituting the very primitive family Psettodidae, are the only flatfishes which are indiscriminately sinistral (with both eyes on the left side) or dextral (eyes right), on a basis which can be interpreted plausibly as primordial (Regan, 1910 : 488). The optic chiasma in this genus is dimorphic (with either left or right nerve the upper one), as it is in fishes in general (p. 285), and left-eyed and right-eyed individuals are said to occur with about equal frequency. We know of no adequate published data on the laterality of this genus. Some authors have described *P. erumei* as dextral, others as sinistral, and there has even been some discussion as to whether the right-eyed and left-eyed individuals represent a single species. Oshima (1927 : 178) listed five sinistral specimens and one dextral from Formosa. The five collected by Carl L. Hubbs at Batavia, Java, in 1929, include two that are sinistral; three, dextral. Twelve specimens from the Philippine Islands and from Batavia, Java, and Hong Kong, China, kindly loaned us by Dr. Leonard P. Schultz of the United States National Museum, comprise three sinistral and nine dextral. The total tally for *P. erumei* (entered in Table I) is therefore ten sinistral and thirteen dextral.

A small group of flounders related to *Citharus* comprises three sinistral genera hitherto placed in the Bothidae and two dextral genera previously classed in the Pleuronectidae (Hubbs, *In press*). In the left-eyed species the nerve of the right eye is dorsal in the chiasma; in the right-eyed forms, the left nerve is superior. There seems to be some obligatory relation between laterality and type of chiasma in this group, for the one known reversed specimen, the dextral individual of *Citharoides macrolepidotus*, referred to below, has the nerve of the left eye dorsal, as it is in the species that are normally dextral. It is suspected that the flounders of the sinistral family Scophthalmidae may show the same relation between the side bearing the eyes and the mode of crossing of the optic nerves.

All flatfishes comprising the four major families are interpreted as normally either dextral or sinistral, whether they be soles (Cynoglossidae and Soleidae), which, though highly specialized in other respects, retain the primitive dimorphic type of chiasma, or flounders and their allies (Bothidae and Pleuronectidae), which have developed a monomorphic chiasma. In all bothids in which the character has been studied the right nerve has always been found to cross dorsally to the left nerve, and the eyes are almost invariably on the left side, whereas in all pleuronectids examined, with the exception of one specimen (pp. 245–246), the left optic nerve has been determined to be dorsal in the decussation, and the eyes and color are normally on the right side. These significant relations between the side bearing the eyes and the type of optic chiasma were discovered by Williams (1902 : 34), and were then thoroughly demonstrated in a classical study by Parker (1903). Parker's conclusions have been widely quoted, as by Jordan (1905, 2 : 482–483) and Ludwig (1932 : 234–237). His results have been extended and confirmed by other workers, including Regan (1910 : 487–488), Mayhoff (1912), Wu (1932 : 46–47), Norman (1934 : 28–29, fig. 19), and Hubbs and Marini (1939 : 159–160). The data have been summarized by Gudger (1935 : 26–35, fig. 5) and Hubbs (*In press*).

Since the location of the eyes is almost invariable in the respective families, the tongue soles (Cynoglossidae) are regarded as normally sinistral; the true soles (Soleidae), as normally dextral. Because of the almost constant position of the eyes in most species, and because of the correlation between the location of the eyes and the

special type of monomorphic chiasma, the turbots (Bothidae) are regarded as normally sinistral; the flounders proper (Pleuronectidae), as characteristically dextral. Specimens with the eyes on the side that is normally blind are said to be reversed. This condition is regarded as abnormal, even for those species or races which often have the eyes on the "wrong" side, including the invariably reversed Asiatic races of one species.

REVERSAL OF SIDES IN FLOUNDERS

Extensive reviews of the problem of reversal in flounders (Ludwig, 1932 : 234–237; Norman, 1934 : 27–29, *et passim;* Gudger, 1935; Hubbs and Kuronuma, 1943 : 298–301) have shown: (1) that sinistral Soleidae are exceedingly rare and that dextral Cynoglossidae are still unknown; (2) that dextrality occurs with extreme rarity in all bothids, except in a very few Pacific species which are said to be indifferently sinistral or dextral; and (3) that sinistrality is so rare as to appear teratological in all Pleuronectidae, except the two species now referred to *Platichthys* and possibly also the North Pacific species *Hippoglossoides elassodon* and the New Zealand genus *Rhombosolea.* Our study proves that *Hippoglossoides elassodon* is now to be removed from the list (pp. 237–238). Adequate data on the proportion of rights and lefts in *Rhombosolea* are not available.

In the European flounder, now known as *Platichthys flesus,* the percentage of reversal varies widely, but usually remains below 50 per cent, as demonstrated by Duncker (1895 : 82–83; 1900 : 339–340), Berg (1932 : 3–7), Ludwig (1932 : 235), Norman (1934 : 28), and Gudger (1935 : 20, 29–30). Geographical variation in laterality that is even more remarkable is exhibited by the Pacific species *P. stellatus,* in which the percentage of reversal is 49 to 60 in western North America, 68 about Kodiak Island and the Alaska Peninsula, and 100 in Japan (Hubbs and Kuronuma, 1942 : 298–301). Since the data for *Platichthys stellatus* are now very extensive, the differences in percentage of reversal between the species of *Platichthys* are certainly not related, as Gudger (1935 : 21) thought that they might be, to the size of the commercial catch.

The reversal of sides in the Japanese population of *Platichthys stellatus* seems to be invariable or at least nearly constant, for all the 476 Japanese specimens examined were sinistral. Hybrids between this sinistral *Platichthys* and the dextral species *Kareius bi-*

coloratus were both sinistral (14) and dextral (13). These data furnish some of the strongest evidence that reversal is genetically determined.

As the foregoing account shows, reversal is a common phenomenon only in Pacific species and in *Platichthys flesus* of Europe. Jordan and Goss (1889 : 230–233, 242–245), Jordan and Evermann (1898 : 2602–2712), Parker (1903 : 231), Jordan (1905, 2 : 481–483, 492), and Regan (1910 : 487) were impressed by the indiscriminate laterality of several flounders along the west coast of the United States. The high frequency of reversal in the flounders of the northeastern Pacific can be explained in part only by the greater development in that region of the groups concerned, namely, the Paralichthyinae and the Pleuronectidae (see zoogeographic analysis by Norman, 1934 : 48–50). It may, of course, be only a series of coincidences (1) that the Pacific species of *Platichthys* is reversed more often than the Atlantic form; (2) that the only species of *Paralichthys* reported to have both eyes commonly on the right side is *P. californicus;* and (3) that among the genera related to *Paralichthys* only eastern Pacific representatives, *Hippoglossina* and *Xystreurys*, are reported to be indiscriminately sinistral or dextral. The almost complete restriction to the Pacific Ocean of the species with aberrant laterality still poses a problem.

Except for *Platichthys stellatus* no statistical data of consequence have been reported on the percentage of reversal among the Pacific species which are claimed to be more or less indiscriminately right-sided or left-sided. Parker's (1903 : 231–232) figures of 11 sinistral (normal) and 15 dextral (reversed) examples of *Paralichthys californicus*, as well as those of 50 dextral (normal) and 50 sinistral (reversed) specimens of *Platichthys stellatus*, though repeated by Ludwig (1932 : 235–236) and by Gudger (1935 : 19–21), probably represented selected samples. Extensive series of counts are called for to determine how "indiscriminate" the sidedness is in the variable Pacific species. A small number of counts are contributed toward this need in Table I. The data for *Psettodes erumei* are discussed on page 234. The data for *Tephrinectes sinensis* are those of Oshima (1927 : 193), who reported 4 sinistral and 3 dextral specimens from Formosa, and of Wu (1932 : 47, fig. 17) who recorded 2 sinistral and 4 dextral examples from China; plus one dextral specimen from Canton, China. *Paralichthys californicus* is almost surely nor-

TABLE I

DATA ON SIDE BEARING EYES IN PACIFIC FLATFISHES REPORTED TO BE MORE OR LESS INDISCRIMINATELY SINISTRAL OR DEXTRAL

Based on material in the Museum of Zoology of the University of Michigan (except as noted in the text). The limited data on *Platichthys stellatus* are a slight supplement to the more than 18,000 counts for this species published by Hubbs and Kuronuma (1942: 299–300). None of the material was selected for sidedness.

Family (and normal condition)	Species and locality	Number of specimens	
		Sinistral	Dextral
Psettodidae (indiscriminate)	*Psettodes erumei*, Philippines, Java, and China	10	13
Bothidae (normally sinistral)	*Tephrinectes sinensis*, Formosa and China	6	8
	Hippoglossina stomata, southern California	3	0
	Paralichthys californicus, southern California	93	57
	Xystreurys liolepis, southern California	9	18
Pleuronectidae (normally dextral)	*Hippoglossoides elassodon*, Frederick Sound, Alaska (shrimp trawls, Sept. 1, 1939)	0	312
	Other localities, Alaska and Puget Sound	0	16
	Platichthys stellatus, California	13	13

mal oftener than reversed; our counts, yielding a P value of 0.003, are 93 sinistral and 57 dextral (part of the material is in the California Academy of Sciences). It is possible that *Xystreurys liolepis*, by contrast, may be more commonly reversed than normal, for the ratio in the material at hand is 9 sinistral to 18 dextral. The allocation of *Xystreurys* in the Bothidae is not to be questioned, for the right optic nerve is the more dorsal (Hubbs and Marini, 1939: 159). Frequent variation in the side bearing the eyes is thus confirmed for all species just mentioned. We find no basis and no confirmation, however, for the statements that *Hippoglossoides elassodon* is "sometimes" or "frequently" sinistral (Jordan and Gilbert, 1883: 826, 827; Jordan and Goss, 1889: 230; Jordan and

Evermann, 1898 : 2605, 2615). If reversal does occur in this species, it must be with rare frequency. The three specimens of *Hippoglossina stomata* listed are all sinistral, as was a specimen recorded previously (Hubbs, 1916 : 168). More data on this genus are greatly needed, since the statements in the literature (Jordan and Goss, 1889 : 230, 242; Jordan and Evermann, 1898 : 2620; Norman, 1934 : 28, 65) are based on very limited material and are somewhat conflicting.

Variability in the location of the eyes is, for some unknown reason, much less common in the northwestern than in the northeastern Pacific. In his elaborate doctoral study of Japanese flounders and soles, based on the extensive collections which Carl L. Hubbs made in 1929, Katsuzo Kuronuma determined, among the hundred species occurring in Japan: (1) that supposedly indiscriminate laterality characterizes only *Psettodes erumei* and *Tephrinectes sinensis*, which barely reach the waters of Japan proper and are unrepresented in the collections made there in 1929; (2) that *Platichthys stellatus* (as already stated) is invariably reversed in Japan; (3) that out of nearly 2,400 specimens, representing the other Japanese species, only two are reversed. The ratio of 1 : 1,200 for reversed : normal individuals of these ninety-seven species may be too high, for the Japanese collectors from whom the specimens were received in 1929 may have preserved both of these reversed flatfish because of their abnormality. One is a dextral example of *Citharoides macrolepidotus*, one of the two Japanese examples at hand of this citharid (Hubbs, *In press*). The other one is the unique sinistral representative (Pl. I, Fig. 2) found among the 201 specimens of the pleuronectid species *Tanakius kitaharae* collected in 1929. The only other known cases of reversal among the flounders of eastern Asia are: (1) a dextral specimen of *Paralichthys olivaceus*, with the right optic nerve dorsal (Wu, 1932 : 47), (2) a dextral example of the bothid species *Pseudorhombus pentophthalmus* (Kamohara, 1935 : 682, fig. 6), and (3) a sinistral *Limandella yokohamae*, with the left optic nerve superior (Wu, 1932 : 47). The reversed specimens recorded by Wu were found in an extensive study of Chinese flatfishes.

The discovery of occasional reversal in five additional species, just mentioned, strengthens the opinion that all species of flounders may occasionally have the eyes and color on the side which is

normally blind and white. Why the phenomenon of reversal is frequent in only a few species remains a total enigma.

DECREASED VIABILITY OF REVERSED FLOUNDERS

There is some evidence that sinistral individuals of normally dextral flounders (*Platichthys*) are less viable than the right-handed ones. Published statements to this effect are based on the following data for *Platichthys flesus* of Europe (Duncker, 1900 : 339–340):

> . . . Apstein [1] fand unter 154 jungen (3,5—8,4 cm langen) Tieren aus der Eckernförder Bucht 56 (= 36,4 %), ich [2] unter 90 gleichfalls jungen (1,9—6,6 cm langen) aus der Neustädter Bucht 31 (= 34,4 %) linksäugige; unter 225 marktreifen [3] Stücken aus der westlichen Ostsee und von der Nähe der Elbmündung erhielt ich dagegen nur 53 (= 23,6 %) linksäugige, sodass der Prozentsatz der letzteren bei den jungen Tieren höher war. Dementsprechend finde ich auch bei dem Plymouth-Material in den drei kleineren der sechs unterschiedenen Grössengruppen linksäugige Exemplare etwas häufiger, als in den drei grösseren (geschlechtsreifen) und zwar bei beiden Geschlechtern in dem nahezu gleichen Verhältnis 1 : 0,85 (♂ = 7,14 : 6,12 %, ♀ = 4,20 : 3,52 %). Unter 192 metamorphosierenden Larven von Megavissey-Harbor waren nur 11 (= 5,73 %) linksäugige, also nicht mehr, als unter dem noch nicht geschlechtsreifen Teil des Materials.
>
> Da eine nachträgliche Veränderung der Augenstellung bei den Plattfischen ausgeschlossen ist, so lässt sich nur auf eine höhere Sterblichkeit der linksäugigen Exemplare gegen die Geschlechtsreife hin schliessen.[4] Ob der von mir gefundene Unterschied der Geschlechter in der Augenstellung — nahezu $1\frac{3}{4}$ mal soviel linksäugige Männchen, wie Weibchen — ein durchgreifender ist, muss einstweilen dahingestellt bleiben.

Duncker's conclusion that the percentage of sinistrality decreases with age in the flounder of the Baltic Sea seems to be statistically valid, provided the results were not greatly affected by local or temporal variation. The ratio of lefts to rights in the young was 87 : 157; in the adults, 53 : 172. The χ^2 value for the difference between these ratios is 8.18, corresponding to a P value of 0.004; that is, there are only 4 chances in 1,000 that the differences in the ratios would have been caused by chance.

Duncker's evidence was confusingly presented by Gudger (1935:

[1] *Mitth. deutsch. Seefischereiver.*, 1894, No. 5.

[2] *Ibid.*, 1897, No. 1.

[3] Ich verstehe unter „marktreif" Tiere von ca. 20 cm Länge und darüber.

[4] Vielleicht ist eine Erfahrung erwähnenswert, die ich kürzlich (Ende Mai 99) mit 67 jungen (1,5—3 cm langen) Elbbutt machte. Für das Aquarium gefangen, erlitten diese 67 Tiere einen längeren Transport in demselben Gefäss unter gleichen Bedingungen; es kamen lebend an 14 links- und 31 rechtsäugige; es gingen unterwegs ein 11 links- und 11 rechtsäugige.

22–23, 29). Apparently misled by the title of Apstein's paper, Gudger attributed to the plaice (*Pleuronectes platessa*) Apstein's figures (1894 : 106) on the percentage of sinistrality in young flounders (*P. flesus*). These were the data utilized by Duncker in the passage just quoted, and they apply without doubt to the flounder. Assuming that they refer to the plaice, Gudger was confronted by a seemingly enormous decrease with age in the number of reversed individuals in that species. To explain the change he postulated an almost complete mortality of the young plaice, but, of course, no amount of nonselective mortality would affect the proportion of reversed to normal individuals. There is no reason to think that young plaice are reversed except with the extreme rarity that characterizes this phenomenon in most flatfishes. Similarly, confirming the statements by Williams (1902 : 34) and Parker (1903 : 230), we find no reversed individuals among more than one hundred transformed young of the related species, the winter flounder, *Pseudopleuronectes americanus americanus* (these specimens, from Massachusetts, grade down to 11 mm. in standard length).

Confirmatory though not fully conclusive evidence on the decreased viability of reversed flounders was kindly furnished us by the late Dr. E. Victor Smith, of the University of Washington (Table II). His extensive data appear to show that the Puget Sound form of the starry flounder, a race of *Platichthys stellatus rugosus*, is slightly oftener sinistral (reversed) when young than when adult. Unfortunately the most acceptable comparison, between the 1928 and 1929 adults and the 1930 and 1931 fish, largely young, both from Boundary Bay, does not yield a statistically reliable result: the ratios of sinistral to dextral fish are 444 : 475 and 254 : 234, respectively; the χ^2 value for the difference in ratios is 1.78, corresponding to a P value of 0.18. A rather highly trustworthy difference exists between the ratios for the Boundary Bay adults (445 : 475) and for the fish, very largely young, taken in the same year about the San Juan Islands (3,436 : 3,151): $\chi^2 = 4.79$ and $P = 0.03$. One cannot exclude with full confidence, however, the possibility that racial, annual, or seasonal variations were responsible for the observed differences. The data in Table II are a breakdown of figures summarized by Hubbs and Kuronuma (1942 : 300). Other counts of normal and reversed individuals of *Platichthys stellatus* published by these authors are too diverse for locality, or too uniform or too

TABLE II

RELATION BETWEEN AGE AND SINISTRALITY IN *PLATICHTHYS STELLATUS* FROM PUGET SOUND

The data were kindly furnished by the late Dr. E. Victor Smith, of the University of Washington. Localities are as follows: (1) San Juan Islands; (2) Boundary Bay; (3) Seattle. More specific data on age are not at hand.

Age	Locality	Year	Number of specimens examined	Percentage reversed (sinistral)	Median
Very large majority in first year	1	1928	1,687	52.22	52.18
	1	1929	4,900	52.14	
Largely in first year, with a few scattered through older years	2	1930	277	52.71	51.95
	2	1931	211	51.18	
Mostly small, but more large fish than in preceding series	3	1929	422	50.47	50.47
	3	1930			
All large, none less than two years old	2	1928	318	49.69	48.64
	2	1929	601	47.59	

indefinite as to age, to bear significantly on the problem of present concern.

The dextral individuals of *Platichthys*, normal in the sense that dextrality is almost universal in the Pleuronectidae, seem to have a slightly better chance than the sinistral ones to reach maturity. It is difficult, but not impossible, to reconcile this interpretation with the evidence (Hubbs and Kuronuma, 1942 : 298–301) that laterality is inherited in *Platichthys stellatus*, that reversal has remained close to 50 per cent on the American west coast for decades, and that reversal is invariable in Japan. Further and more detailed data on the proportion of left-eyed to right-eyed individuals in the young of the starry flounder, particularly in recently transformed young, are still a great desideratum, as Gudger (1935 : 21–22) wrote. So far as possible, in such studies efforts should be made to eliminate the factors of racial, annual, and seasonal variation, which were not completely excluded in the accumulation of the data discussed above.

The supposedly decreased viability of reversed flounders has been cited by Parker (1903 : 229–238), Mayhoff (1912 : 84–85), Norman

(1934 : 28), and others as evidence that the monomorphic chiasma arose as a product of selection. The extreme twisting of the optic nerves in reversed bothids and pleuronectids has been stressed by Parker and subsequent workers as a mechanical disadvantage; the monomorphic chiasma of the Bothidae and the Pleuronectidae is interpreted as allowing a simple and direct ontogeny. The dorsal location of the nerve of the migrating eye in both groups leads in the normal (unreversed) individuals to a partial uncrossing rather than a double crossing of the optic nerves. Such adaptations toward direct development are frequent — whatever the evolutionary mechanism may be. But if sinistrality in the Bothidae and dextrality in the Pleuronectidae arose because these conditions have a selectional advantage, why has reversal of sides become common in several species of Bothidae and in both species of *Platichthys?* In particular, we may well ask, Why has *Platichthys stellatus* become invariably reversed in eastern Asia?

Whatever may be its evolutionary basis, reversal of sides in the flounder families with a monomorphic chiasma is surely to be regarded as a secondary development (Parker, 1903 : 234; Norman, 1934 : 28). Ambilaterality is obviously both primitive and common only in the Psettodidae, and presumably remains primitive, though it has become rare in the Soleidae and also in the Citharidae and probably in the Scophthalmidae (Hubbs, *In press*).

INCOMPLETE MIRROR IMAGING IN REVERSED FLOUNDERS

One of the most remarkable features of variation in the side of flounders bearing the eyes is the lack of complete mirror imaging (the one completely reversed specimen described on pp. 245–246 provides an exception to this statement and to each of the following generalizations in this section). On superficial examination dextral and sinistral examples of the same species do appear to be mirror images, and indeed they were commonly so regarded prior to 1903, but closer inspection has shown that certain structures exhibit no reversal. Thus, as already pointed out (p. 235), it has been demonstrated adequately that the right optic nerve is invariably dorsal in all Bothidae and that the left nerve is dorsal in all Pleuronectidae, without respect to the side bearing the eyes. The monomorphic asymmetry is established prior to metamorphosis (Williams, 1902 : 34; Parker, 1903 : 230; Jordan, 1905, 1 : 174).

That the viscera in the flatfishes constantly maintain the bilaterally asymmetrical arrangement that is characteristic of fishes in general, with the liver on the left side and the intestinal coils against the right body wall, has already been determined (Cunningham and MacMunn, 1894 : 801; Cunningham, 1907 : 176; Norman, 1934 : 29). I have verified this conclusion by an examination of numerous flounders, including both dextral and sinistral specimens of: (1) *Psettodes erumei*, a species of the Psettodidae, in which neither side can be said to be normal, neither reversed; (2) *Citharoides macrolepidotus*, one of the ordinarily sinistral species of the Citharidae; (3) *Paralichthys californicus* and *Xystreurys liolepis*, members of the normally sinistral family Bothidae; and (4) *Platichthys stellatus*, representing the normally dextral Pleuronectidae. The typical pattern of asymmetry holds for both dextral and sinistral individuals of *P. stellatus* on the American west coast and for the exclusively sinistral Japanese race; also for the dextral and sinistral hybrids between *Kareius bicoloratus* and *Platichthys stellatus*. Hubbs and Kuronuma (1942 : 295–298) obviously drew up their description of the visceral anatomy of these species and the hybrids from sinistral specimens and wrongly indicated that this pattern holds also for the dextral hybrids and *Kareius;* for those forms the term "blind side" in the published account should have read "right side" or "eyed side." It is obvious that the more fundamental features of visceral asymmetry are fixed prior to metamorphosis, in the pattern that is characteristic of fishes in general.

There is at least one other bilateral asymmetry in certain flatfishes that maintains a constant pattern unrelated to the general twisting of the head and body. In representative specimens of the few flatfishes in which these folds remain separate, instead of being symmetrically conjoined (Schmidt, 1915 : 442–443; Hubbs, *In press*), we find that the right branchiostegal membrane embraces the urohyal and is covered by the more deeply pigmented left membrane. This is true of *Psettodes erumei* and of *Citharoides macrolepidotus*, whether the specimen be dextral or sinistral in respect to eyes and color. The left membrane also overlaps the right in another sinistral citharid, *Citharus macrolepidotus*, as well as in the dextral citharid *Brachypleura novae-zeelandiae*. The left membrane is also constantly the outer one in *Lophopsetta aquosa* and other Scophthalmidae, of which only sinistral specimens are known. We

conclude that this asymmetry in the folding of the gill membranes must be established very early in the life of these flatfishes, prior to metamorphosis. In fact, the pattern was established very early in the evolution of modern fishes: the left membrane overlaps the right in *Amia calva*, and this condition is more or less definitely retained throughout the teleost series (Hubbs, 1920 : 62, see also pp. 278–280 of the present paper).

A COMPLETELY REVERSED FLATFISH

An exception to the rule that there is no complete reversal of bilateral parts in flounders is furnished by the one known sinistral example (Pl. I, Fig. 2) of *Tanakius kitaharae* (Jordan and Starks), a Japanese species of the normally dextral Pleuronectidae (Pl. I, Fig. 1). This specimen, already referred to (pp. 235, 239), is an adult 220 mm. in standard length. It was collected in the Pacific Ocean off Onahama, Japan, by the Fukushima-ken Fishery Experiment Station, and was presented to Carl L. Hubbs in Japan in 1929.

In all essential respects this sinistral example seems to be the mirror image of a normal *Tanakius*. The intestine projects into the backward extension of the coelome on the left side, rather than on the right side, as it normally does in this and several other genera, without any hitherto known exception. The liver is on the right side, rather than on the left, as it is in all other flatfishes so far as previously determined, whether they be dextral or sinistral. The intestinal coils are on the left side, rather than the right, as in all other known specimens. This is the general rule for fishes. Situs inversus viscerum is presumably rare among the Pisces, although Lynn (1943) recorded an incidence of 4.7 per cent among 510 single embryos of trout and a higher percentage among conjoined twins. Ludwig (1932 : 379) quoted data on situs inversus in amphibians, but not in fishes.

Suspecting that this fish might represent a complete reversal, we examined the crossing of the optic nerves. The right nerve was found to pass dorsally to the left nerve, a position never recorded in a pleuronectid, either normal or reversed. The optic nerves cross but once, instead of twice, as they do in all other known reversed flounders, with one exception, whether they be referable to the Pleuronectidae or to the Bothidae (Hubbs, *In press*). In this

respect the reversed *Tanakius* agrees with the reversed (dextral) *Citharoides*, but that fish (p. 235) retains the normal asymmetry of viscera and of branchiostegal membranes. The appearance is that of a sinistral specimen of the typically sinistral Bothidae, as represented by Parker's often reproduced figure 5 (1903) or by Mayhoff's figure 3 (1912), rather than that of a reversed example of the normally dextral Pleuronectidae. It seems certain, however, that this specimen is not a bothid, for it is obviously a reversed individual, and all its characters stamp it as an aberrant member of the pleuronectid species *Tanakius kitaharae*.

This specimen provides the first known exception to the rule that the optic chiasma is invariably monomorphic in the Bothidae and Pleuronectidae. It furnishes the first known case, for either family, of the mirror imaging of the chiasma. That the left optic nerve is normally the more dorsal in *Tanakius kitaharae* was demonstrated by the dissection of ten dextral specimens.

In the more usually observed asymmetrical characters this specimen is also reversed. The blind side is nearly colorless and is less muscular than the ocular side. The urinary papilla is on the eyed surface. The head parts are just the reverse of normal.

In two other respects the completely reversed *Tanakius* specimen is slightly teratological. The posterior end of the dorsal fin is somewhat deflected onto the blind side, instead of retaining, as usual, a position along the median dorsal line. On the eyed side of the abdomen, an isolated segment of the lateral line, with well-developed pored scales, extends upward for some distance from between the pelvic fin and the anus.

It seems obvious that reversal is more fundamental in this specimen than in any other known flatfish.

INTERPRETATION OF REVERSAL IN FLATFISHES

A reversed symmetry of the early embryo or egg — involving some embryonic structure or position, the direction of cell cleavage, or the constitution of the egg itself — probably accounts for the complete change-over of right and left elements in the specimen just described, but seems not to be involved in the ordinary reversal of sides in the Heterosomata. No other specimen of flatfish is known to have all its organs reversed. Usually in two and sometimes in three characters reversed flatfishes are not perfect mirror images

of normal specimens. The asymmetries of the optic chiasma in the Bothidae and the Pleuronectidae, of the viscera in all flatfishes, and of the gill membranes in several genera (pp. 243–245), obviously become established in a pattern which is unrelated to the later twisting of the head. These almost invariable asymmetries must be fixed very early in development, for certain flatfishes metamorphose at a small size (data on the size at transformation were summarized by Norman, 1934 : 30–33). The types and degree of asymmetry seem to bear little relation to the size at which one eye migrates to the opposite side of the head. Some flatfishes, particularly the tropical Bothidae, transform at a surprisingly large size. The record case is that of *Laeops parviceps*, of which there has been described a postlarva 70.5 mm. in standard length, with one eye still on each side of the head (Hubbs and Chu, 1934 : 3–6, pl. 2).

The one completely transformed specimen of *Tanakius* is, therefore, the only reversed flatfish that is fundamentally comparable to sinistrally coiled snails. Reversal in the Gastropoda has been traced to a 180° change in the direction of cell cleavage. The literature on reversal of coiling in gastropods was reviewed at length by Ludwig (1932 : 159–191, figs. 103–105).

Sinistrality in normally dextral flounders and dextrality in those that belong to the sinistral groups are no more related to situs inversus of the viscera in flatfishes than left-handedness is associated with situs inversus in man.

A number of authors, including Cunningham (1907 : 175–176), Gudger (1935 : 35), and Hubbs and Kuronuma (1942 : 301), have concluded that laterality, whether normal, reversed, or variable, is genetic. The facts of the case (p. 237) lead very strongly to this conclusion. The production of rights and lefts in approximately equal numbers, in the hybrids derived from the natural crossing of the dextral species *Kareius bicoloratus* and the invariably sinistral Japanese races of *Platichthys stellatus* (Hubbs and Kuronuma, 1942 : 300), suggests strongly that simple genetic factors are involved in determining whether a flounder be left-eyed or right-eyed. There is no evidence that cytoplasmic inheritance is operative in the development of flatfish asymmetry.

From the viewpoints both of bionomics and of developmental mechanics many theories have been advanced to explain why some

flatfishes lie on the left side, others on the right. Involved theories have been published, by Ludwig (1942 : 237), for example, to explain how unilaterality became established and how reversal has taken place. Lamarckian factors have been stressed by many of the theorists. None of the hypotheses proposed has met with any general acceptance (Norman, 1934 : 13, 31). Most of the attempted explanations have some unacceptable or unprovable basis. As a whole, these proposals have transcended factual information and have merely added confusion to a difficult puzzle.

The one interpretation that has been generally agreed upon, since Parker's work was published in 1903, is that reversal is a secondary and not a primary feature, except in *Psettodes*. This conclusion seems to be warranted both for the soles, which retain the primitive dimorphic chiasma, and for the Bothidae and Pleuronectidae, which have a monomorphic decussation of the optic nerves. It may be questioned for the members of the small families Citharidae and Scophthalmidae (Hubbs, *In press*).

Whether or not reversed flounders are to be regarded as teratological depends in part on the point of view (Gudger, 1935). It has been noted, however, that reversal of the sides often occurs in flounders that have other abnormalities, such as ambicoloration and partial albinism. Gudger (1935) referred to a number of such specimens, including the exceedingly abnormal turbot reported by Cunningham (1907), and has since described three specimens combining reversal with ambicoloration (Gudger, 1936a; Gudger and Firth, 1937). The completely reversed specimen of *Tanakius kitaharae* recorded above shows other anomalies (p. 246). In the New Zealand genus *Rhombosolea* reversal is usually accompanied by the reappearance of the normally lacking pelvic fin of the blind side, according to Norman (1926 : 278–280; 1934 : 28–29). In species which are rarely reversed there is apparently some association between reversal of sides and other abnormalities, particularly ambicoloration. Since the coloring of both sides is interpreted as a return toward symmetry (see following section), it may be that this return is often carried beyond the mid-point, so as to lead to a change in the side bearing both eyes. In view of the data given in the next paragraph this is a more plausible idea than that the reversal of the sides leads to ambicoloration.

It seems to be significant, in this connection, that such anomalies

as ambicoloration are apparently no more common in the several North Pacific flounders which are notable for their indiscriminate laterality than they are in species which always or almost always have the eyes and color on one of the sides. None of the reversed specimens listed in Table I showed any sign of ambicoloration or other abnormality. We have heard of only three cases of ambicoloration in *Platichthys stellatus*, the flatfish with the record proportion of reversals, and only one of these reports rests on a specimen, a dextral individual from southeastern Alaska that was described by Gudger (1941). One hearsay record was mentioned by Gudger, and we can now add a third report. Silva, the long-time fisherman of Morro Bay, California, described to us personally what was certainly another ambicolorate *Platichthys*, "the same on both sides." These three teratological individuals are the only ones which have been noticed by men who have handled many thousands of starry flounders. Among the 476 specimens examined of the invariably sinistral Japanese race not one presented any obvious anomaly. There is no reason to think that ambicoloration and other terata are any commoner in *Platichthys stellatus*, which varies geographically from a condition of indiscriminate laterality to one of complete reversal, than they are in flatfish species that are never or virtually never reversed.

TERATOLOGICAL RETURN TOWARD SYMMETRY

The teratological condition of flatfishes known as ambicoloration, with related modifications, has been interpreted as a return toward the symmetrical structure of ordinary fishes. Not only the color but also other characters of the eyed side, for example, ctenoid scales, may appear on the eyeless side. The migrating eye may not have rotated the usual distance, and the forward extension of the dorsal fin, which ordinarily follows the transit of the eye, may not have been completed. As a result, a dorsal hook is commonly developed in extreme examples of ambicoloration. The subject was treated at some length, with a review of the literature, by Norman (1934 : 22–27, figs. 18–19), and more recently has been extensively investigated by Gudger (1935, 1936a, 1936b, 1941; Gudger and Firth, 1935, 1936, 1937).

Although numerous ambicolorate flatfish have been described, the condition must be extremely rare. The aberration is so striking

that it has often come to the attention of zoologists. Numerical data on the relative frequency of ambicoloration have not been published. It may be of interest, therefore, to note that among the 2,412 specimens of Japanese flounders handled by Katsuzo Kuronuma (doctoral thesis, University of Michigan, probably still unpublished), only three were colored on both sides, and these may have been preserved because of their abnormality. Two of the specimens are of *Verasper variegatus*, a species that usually has scattered dark spots on the lower surface. One of the two has the hooked dorsal fin commonly associated with ambicoloration. The other *Verasper* and the one ambicolorate specimen of the abundant species *Limandella yokohamae* have a normal dorsal fin.

SECONDARY ASYMMETRIES IN FLATFISHES

Although there are a few basic asymmetries that maintain a left–right gradient unaltered by the reversal of the sides, the majority of the head and body characters develop bilateral dissimilarities along with or following the migration of the eye. Profound differences, for example, arise between the corresponding left and right elements in the skeleton and the musculature. Many of these secondary asymmetries have been described, and efforts have been made to interpret the findings (Norman, 1934: 1–55, figs. 1–28). Some have argued that the migration of the eye directly causes the excessive twisting of the anterior part of the skull; others have regarded the flexure of the skull as the primary movement, which carries the eye along with it. Objections have been raised, however, to any such simple cause-and-result relationship. In modern view it seems much more plausible to assume that a multitude of factors is involved, and that the whole genetic and developmental mechanism is keyed to the production of an organism that is asymmetrical in almost every element of internal and external anatomy.

Next to the unilateral position of the eyes, the bilateral difference in color is the most conspicuous feature in the asymmetry of the Heterosomata. In most flatfishes whichever side is blind is white, and almost entirely devoid of melanophores, whereas the upper side is thoroughly equipped with chromatophores. These color cells expand and contract as the exposed side marvelously simulates the color and the color pattern of the bottom on which the fish lies (references in Norman, 1934: 21).

Not all flatfishes, however, are unpigmented on the lower surface. In the primitive, relatively not greatly asymmetrical species *Psettodes erumei* we note a slight darkening of the under side. Similarly, a gray shade covers this side in the secondarily subsymmetrical flounders, such as *Atheresthes*. One such form first loses, then regains pigment on the under surface (Norman, 1934 : 21). Oddly, some of the more or less extremely asymmetrical flounders, such as certain species of *Glyptocephalus, Taeniopsetta, Engyophrys,* and *Verasper,* develop dark pigment on the blind side, either as a shade or as a pattern of bars or spots. The adult male of *Crossorhombus kobensis,* a Japanese bothid, has a large violet wedge on the lower surface (Hubbs, 1915 : 459). The dark spots on the lower surface of the "hogchoker," an American sole, are almost wholly confined to *Trinectes maculatus maculatus*, the northern subspecies (Hubbs and Allen, 1944 : 128). Such variations in the pigmentation of the side on which the flatfishes lie are not readily explainable.

Since it was shown by Cunningham (1891, 1893, 1895; Cunningham and MacMunn, 1894) that flatfishes illuminated from below develop pigment on the normally white skin, some have thought that the lack of color is the direct result of the absence of light. Cunningham found, however, that heredity is involved, for in early development the pigment of the illuminated blind side first disappeared, "and it was only later after long exposure to light that pigment developed on the lower side."

In many flounders the lateral line is developed only on the eyed side, or is better developed there. Basic data are a part of the systematic literature (reviewed by Norman, 1934). In the best statistical analysis of this asymmetry Duncker (1900 : 374–375, 392; 1904 : 576–578, 646–647, 653) demonstrated that the accessory branch of the lateral line of *Platichthys flesus* averages longer on the ocular side than on the blind side. Quantifying the length of the line by listing the number of the dorsal ray opposite which the line ended, Duncker determined for 1,024 dextral specimens that the length was alike on the two sides in 590 fish, greater on the eyed (right) side in 279, and greater on the blind (left) side in only 155. In sinistral (reversed) flounders the degree of asymmetry was approximately the same, but the direction was altered: the accessory lateral line was usually longer on the left surface. In both cases the greater development was on the side that bears the eyes.

The perfection of scale development on the two sides of flounders is another character that is associated in some way with the direction taken by the migrating eye in metamorphosis. Commonly the scales of the upper side are ctenoid, whereas those of the opposite surface are cycloid (see systematic literature, especially Norman, 1934). Again it is not a problem of which side is right or which is left, but, rather, a question of which half of the body bears both eyes and which half has none. That definite hereditary factors are involved is clearly indicated by the manner in which the tubercular scales are developed on the blind side — whether left or right — in *Kareius* × *Platichthys* hybrids (Hubbs and Kuronuma, 1942 : 278–287, pl. 4).

An asymmetrical location of either the anus or the urinary papilla, and usually of both these structures, is also correlated with the general somatic asymmetry established at metamorphosis. Schmidt (1915 : 444), as quoted by Norman (1934 : 19), "has drawn attention to the asymmetrical position of the anal papilla, which in all flatfishes, including those in which the vent is placed on the blind side, is situated on the ocular side of the median line." We have confirmed this finding for numerous species. The only species that we have found to furnish an exception to Schmidt's rule are the primitive flounder *Psettodes erumei*, in which a urogenital papilla lies close to the anus, in the same fossa, slightly on the blind side and in line between the anus and the front of the anal fin, and the members of three American bothid genera (*Citharichthys*, *Etropus*, and *Syacium*), in which both the papilla and the anus are deflected onto the blind side (Hubbs, *In press*). In dealing with *Platichthys flesus* Duncker (1895 : 81) pointed out that the papilla is the urogenital opening in the males but only the urinary opening in ripe females, and we observe the same situation in *Tanakius kitaharae*. Duncker found the papilla on the blind side in only one specimen of *P. flesus*, among very many studied, and mentioned that Gottsche made a similar observation on one plaice that was white on both sides. Hubbs (1915) noted that the anus of flatfishes in general either lies on the mid-ventral line or is more or less transposed to the blind side, except in *Citharoides* and *Citharus*. In a thorough survey of this character throughout the pleuronectoid flatfishes Norman (1934) determined, in confirmation, that the anus is usually more or less displaced onto the blind side, and lies definitely on the eyed

side only in the two genera just mentioned. In *Citharoides*, as in its close relative *Citharus*, the urinary papilla arises on the edge of the anal opening on the eyed side of the body (in the reversed fish as well as in the normal specimens at hand); in another citharid, *Brachypleura*, the two organs are also on the eyed side, but are slightly separated (Hubbs, *In press*). In all bothids and in all pleuronectids examined the anus and the urinary papilla are separated from each other by a considerable expanse of body surface.

A test was made of the conclusion that the location of the urinary papilla is consistently correlated with the eyedness or blindness rather than with the sinistrality or dextrality of the sides. In more than two hundred specimens of *Platichthys stellatus*, nearly equally divided between rights and lefts, the papilla was on the eyed side without exception. In all the specimens the anus was on the blind side. Similar findings were obtained on normal and reversed specimens, though in smaller numbers, of *Paralichthys californicus* and of *Xystreurys liolepis*.

Unlike the major features of visceral topography, which early develop a gradient of asymmetry unrelated to that taken by the eyes, the posterior openings of the kidney and the intestine have, therefore, an asymmetry that is quite consistent with that of the eyes and color. Apparently the positions of the urinary papilla and of the anus are among the numerous characters that are fixed subsequent to metamorphosis.

Likewise, in some flatfishes marked asymmetries correlated with the position of the eyes appear in the area of the gill covers; this region may be larger or more posterior or otherwise different on one side than on the other. These differences between the two surfaces are reversed when there is a change-over in the position of the eyes. In this respect the superficial gill-cover structures do not follow the monomorphic asymmetry of the branchiostegal membranes and rays (p. 244), which is obviously established earlier in development.

An interesting asymmetry involving the presence of a bone on one side and its absence on the other is exhibited by *Citharoides macrolepidotus*. In this species the supplementary maxillary bone is developed consistently on the blind side but is lacking on the ocular surface.

In the three genera of the Citharidae examined, namely, *Citharus*, *Citharoides*, and *Brachypleura*, a peculiar asymmetry is evident in

the structure of the pectoral fin rays. In the fin of the eyed side the articulations of the rays are much longer than broad, whereas in the blind-side fin the joints of the rays are much broader than long (Hubbs, *In press*). An approach toward this condition is shown by some other flatfishes, including *Psettodes erumei*.

In almost all flatfishes the paired fins are larger and otherwise better developed on the eyed side than on the blind side — whether the eyed side be left or right, and whether the specimen be normal or reversed in respect to the position of the eyes. The supporting data fill the systematic literature on the Heterosomata (ably reviewed by Norman, 1934). It was concluded by this ichthyologist (p. 20) that the pectorals in some flounders are subequal, and, as an exception to the general rule, we find that *Psettodes* usually has the pectoral fin of the blind side the larger (p. 257). In a number of genera of both flounders and soles the pectoral or pelvic fin of the ocular side may be well developed when its mate of the blind side is rudimentary or totally lacking. In these genera, of course, there is a constant difference in the number of pectoral or pelvic rays on the two sides. Bilateral variation in the number of rays in the paired fins, in species of flatfishes having these fins well developed on both sides, calls for special treatment.

BILATERAL VARIATION IN NUMBER OF RAYS IN PAIRED FINS ON THE TWO SIDES OF FLATFISHES

When, as usual, the paired fins of flatfishes are developed on both sides, the fin of the eyed surface as a general rule has on the average a higher number of rays than does the corresponding fin of the blind side — whether the eyes face to the left or to the right. The first and still the most thorough statistical demonstration of this secondary asymmetry was made by Duncker (1897 : 819–820; 1900 : 356–357, 362; 1904 : 630–633; data reviewed by Ludwig, 1932 : 6–8). In *Platichthys flesus* Duncker found that in the normal or dextral individuals the right pectoral nearly always contains more rays than the left fin; that the number of pelvic rays when different on the two sides is higher on the right side in the ratio of about 2 : 1; and that the differences are accentuated, when only the branched rays are enumerated (data reanalyzed in Tables III–IV). In sinistral or reversed individuals the left fin (now on the eyed side) has the higher number of rays; the asymmetry is almost the

TABLE III

AVERAGE NUMBER OF PECTORAL AND PELVIC RAYS ON THE LEFT AND RIGHT SIDES OF DEXTRAL AND SINISTRAL FLOUNDERS (*PLATICHTHYS FLESUS*)

Based on 1,060 dextral and 60 sinistral specimens, from Plymouth, England; data from Duncker (1900: 356). The averages for the right fin are in bold-faced type.

	Eyed side, average	Blind side, average
Total pectoral rays		
Dextral specimens	**10.804**	10.143
Sinistral specimens	10.800	**10.217**
Branched pectoral rays		
Dextral specimens	**6.215**	2.529
Sinistral specimens	6.373	**2.746**
Total pelvic rays		
Dextral specimens	**5.983**	5.960
Sinistral specimens	6.033	**5.950**
Branched pelvic rays		
Dextral specimens	**0.778**	0.276
Sinistral specimens	0.800	**0.350**

same in degree, but reversed in direction. Obviously the correlation is not with the rightness or the leftness of the side but, rather, with eyedness or blindness.

Confirmatory results (Tables IV–V) were obtained in an analysis of the number of pectoral and pelvic rays on the eyed and blind sides of normal and reversed starry flounders, *Platichthys stellatus rugosus*. The counts were all made on specimens collected in the Columbia River mouth, Oregon and Washington, on July 20–21, 1926. The series of 225 specimens comprises 89 normal (dextral) and 136 reversed (sinistral) individuals. Since none of the fish were adult and most were small, the counts were made under a microscope and, when necessary, the skin was cut to make sure that the smallest rudiments were included. The counts of branched rays are valid for the bilateral comparison for specimens of this size, but do not equal the counts that would be obtained from adult fish, since additional rays dichotomize with increasing size. Perhaps in larger fish a significant difference between the eyed and the blind sides might be demonstrated in the number of branched pelvic rays, to conform with Duncker's results on *P. flesus*. There

TABLE IV

ASYMMETRY IN NUMBER OF RAYS, TOTAL AND BRANCHED, IN FLOUNDERS OF THE GENUS *PLATICHTHYS*

L signifies that the count is higher on the left side; *R*, that the count is higher on the right side.

	N	*L*	*R*	$\frac{100\ (L+R)}{N}$	$\frac{100\ R}{L+R}$	100 *P*
Platichthys flesus *						
Dextral specimens						
Pectoral rays						
Total	1,059	17	661	64	97	0.00 †
Branched	1,014	2	992	98	100	0.00
Pelvic						
Total	1,056	20	41	6	67	1
Branched	1,054	31	425	43	93	0.00
Platichthys stellatus rugosus ‡						
Dextral specimens						
Pectoral rays						
Total	89	3	40	48	93	0.00
Branched	89	0	89	100	100	0.00
Pelvic rays						
Total	89	2	3	6	60	...
Branched	89	1	1	2	50	...
Sinistral specimens						
Pectoral rays						
Total	136	57	5	46	8	0.00
Branched	136	135	0	99	0	0.00
Pelvic rays						
Total	136	10	3	10	23	10
Branched	136	5	0	4	0	7

* Data from Duncker (1904: 647–648), for specimens from Plymouth, England.

† A 100 *P* value of 0.00 indicates that the odds are less than 1 in 20,000 that the result obtained is due to chance.

‡ Original data, for young specimens from the mouth of the Columbia River, Oregon and Washington, collected July 20–21, 1926.

is a greater difference between the pelvic rays of the two fins than the figures indicate, because in a number of specimens with the same count in the right and the left pelvic the fin of the blind side only has the last ray rudimentary. As in *P. flesus*, the differences in the pectoral ray counts are much greater for the number of branched

TABLE V

DIFFERENCES BETWEEN PECTORAL RAY COUNTS OF THE TWO SIDES IN DEXTRAL AND SINISTRAL SPECIMENS OF *PLATICHTHYS STELLATUS RUGOSUS*

Based on 89 dextral and 136 sinistral specimens collected July 20–21, 1926, in Columbia River mouth.

	Excess of count of eyed side over that of blind side										*M*
	−1	0	1	2	3	4	5	6	7	8	
Total rays											
D *	3	46	36	4	..	..	..	..	..	..	0.46
S †	5	74	52	3	1	1	..	..	..	..	0.44
Branched rays											
D *	..	..	..	4	11	18	17	24	14	1	5.03
S †	..	1	..	9	16	25	33	34	11	7	4.91

* Dextral (normal) specimens, with the right count (that of eyed side) typically higher than the left count.

† Sinistral (reversed) specimens, with the left count (that of eyed side) typically higher than the right count.

rays than for the total number of rays (Table V). This differential seems to hold for flounders in general, with at least one outstanding exception: in *Xystreurys liolepis* the rays are branched in the pectoral fin of the blind side (either right or left), but remain unbranched in the long straplike pectoral of the ocular side (Hubbs and Marini, 1939 : 162). The mean difference between the counts of dichotomized rays on the two sides is nearly the same in the dextral and sinistral specimens, showing again that the number of rays is correlated with eyedness or blindness rather than with rightness or leftness.

The conclusion that eyedness of the side is correlated with the differential development of the paired fins among flatfishes in general is verified by systematic descriptions and, more particularly, by a statistical study of the Japanese species (Table VI). The outstanding exception to the rule appears, from this tabulation, to be provided by the most primitive of all the flounders, *Psettodes*, which has a dimorphic optic chiasma and one eye on the top of the head. In *Psettodes erumei* the fin of the blind side seems to have the higher average ray count, almost surely not a lower average. The blind-side fin also averages the larger and the stronger (this is true in four-

TABLE VI

FREQUENCY DISTRIBUTIONS OF RAY COUNTS OF THE TWO PECTORAL FINS IN JAPANESE PSETTODID, CITHARID, BOTHID, AND PLEURONECTID FLATFISHES

The counts were made by Research Assistant Katsuzo Kuronuma on material which Carl L. Hubbs collected in Japan in 1929. Supplementary counts for *Psettodes erumei* and *Citharoides macrolepidotus* are added. All the counts for the *Psettodes* are of specimens from Java, the Philippines, and China. Of the nine specimens of the *Citharoides* counted two only are from Japan; the others, from the Philippines. Counts of eleven other Japanese species, omitted because of inadequate series, stand in agreement with those included. The t values are the differences between the means (mean for ocular side minus mean for blind side) divided by the standard error of the difference.

	Number of pectoral rays									$M \pm SE$	t	100 P
	7	8	9	10	11	12	13	14	15			
PSETTODIDAE (indiscriminate laterality)												
Psettodes erumei												
Ocular side	..	..	..	..	..	..	1	10	6	14.29 ± .14	− 1.45	15
Blind side	..	..	..	..	..	..	1	5	11	14.59 ± .15		
CITHARIDAE												
Citharoides macrolepidotus												
Ocular side	..	..	..	9	..	..	..	..	..	10.00 ..	..	..
Blind side	..	..	..	8	1	..	..	..	..	10.11 ..		
BOTHIDAE (sinistral)												
Paralichthys olivaceus												
Ocular side	..	..	..	6	33	41	13	..	..	11.66 ± .08	3.08	0.2
Blind side	..	..	..	14	43	26	7	..	..	11.29 ± .09		
Pseudorhombus arsius												
Ocular side	..	..	..	..	2	10	..	..	..	11.83 ± .11	2.81	1
Blind side	..	..	..	2	6	4	..	..	..	11.17 ± .21		

Pseudorhombus cinnamomeus												
Ocular side	..	..	..	..	3	22	4	..	..	12.03 ± .09	3.76	0.02
Blind side	..	..	..	3	12	13	1	..	..	11.41 ± .14		
Pseudorhombus pentophthalmus												
Ocular side	..	..	..	9	133	106	3	..	..	11.41 ± .04	21.86	0.00
Blind side	..	..	50	126	71	4	..	..	..	10.12 ± .05		
Tarphops oligolepis												
Ocular side	..	..	1	33	12	1	..	..	..	10.28 ± .08	10.76	0.00
Blind side	2	9	29	7	..	..	..	..	..	8.87 ± .10		
Arnoglossus tenuis												
Ocular side	..	..	..	1	6	5	1	..	..	11.46 ± .22	7.50	0.00
Blind side	1	4	4	4	..	..	..	..	..	8.85 ± .27		
Engyprosopon grandisquama												
Ocular side	..	..	..	4	8	..	..	..	..	10.67 ± .14	9.70	0.00
Blind side	..	..	11	1	..	..	..	..	..	9.08 ± .08		
Crossorhombus kobensis												
Ocular side	..	..	3	22	21	2	..	..	..	10.46 ± .10	10.16	0.00
Blind side	..	3	33	12	..	..	..	..	..	9.19 ± .08		
Laeops kitaharae												
Ocular side	..	..	..	..	..	2	9	1	..	12.92 ± .15	5.18	0.00
Blind side	..	..	..	1	5	5	1	..	..	11.50 ± .23		
PLEURONECTIDAE (dextral)												
Atheresthes evermanni												
Ocular side	..	..	..	..	..	..	4	5	4	14.00 ± .23	− 0.06	95
Blind side	..	..	..	..	..	..	2	6	4	14.17 ± .21		
Hippoglossoides dubius												
Ocular side	..	..	9	45	12	..	..	..	..	10.05 ± .07	3.17	0.2
Blind side	..	..	23	38	5	..	..	..	..	9.73 ± .07		
Cleisthenes pinetorum												
Ocular side	..	..	2	36	126	75	9	..	..	11.21 ± .05	2.35	2
Blind side	..	1	6	51	121	61	8	..	..	11.04 ± .05		

TABLE VI (*Concluded*)

	Number of pectoral rays									$M \pm SE$	t	$100\,P$
	7	8	9	10	11	12	13	14	15			
PLEURONECTIDAE (dextral, *Cont.*)												
Xystrias grigorjewi												
Ocular side	..	..	..	30	125	17	..	..	..	$10.92 \pm .04$	0.19	85
Blind side	..	..	1	24	136	11	..	..	..	$10.91 \pm .04$		
Verasper variegatus												
Ocular side	..	..	..	2	17	7	1	..	..	$11.26 \pm .13$	− 0.37	71
Blind side	..	..	..	3	13	10	1	..	..	$11.33 \pm .14$		
Verasper moseri												
Ocular side	..	..	1	..	1	9	1	2	..	$12.07 \pm .32$	0.21	83
Blind side	..	..	..	..	1	12	1	..	..	$12.00 \pm .10$		
Clidoderma asperrimum												
Ocular side	..	..	..	..	..	5	7	5	..	$13.00 \pm .19$	2.54	1
Blind side	..	..	..	..	2	7	8	..	..	$12.35 \pm .17$		
Pleuronichthys cornutus												
Ocular side	..	..	13	59	69	7	..	..	..	$10.47 \pm .06$	1.29	20
Blind side	..	..	16	70	55	7	..	..	..	$10.36 \pm .06$		
Lepidopsetta mochigarei												
Ocular side	..	..	1	3	11	18	2	..	..	$11.49 \pm .14$	1.85	6
Blind side	..	..	2	7	13	12	1	..	..	$11.09 \pm .16$		
Limanda punctatissima												
Ocular side	..	..	9	3	..	..	..	..	..	$9.25 \pm .13$	3.38	0.1
Blind side	..	5	7	..	..	..	..	..	..	$8.58 \pm .15$		
Limandella herzensteini												
Ocular side	..	..	11	55	38	4	..	..	..	$10.32 \pm .07$	4.74	0.00
Blind side	..	1	29	63	13	2	..	..	..	$9.87 \pm .07$		

Limandella yokohamae												
Ocular side	..	..	5	89	127	23	..	..	..	10.69 ± .04	3.28	0.1
Blind side	..	2	11	118	95	18	..	..	..	10.48 ± .05		
Dexistes rikuzenius												
Ocular side	..	1	8	52	9	..	..	..	..	9.99 ± .07	1.65	10
Blind side	..	..	16	49	5	..	..	..	..	9.84 ± .06		
Microstomus achne												
Ocular side	..	1	1	17	4	..	..	..	..	10.04 ± .13	2.60	0.9
Blind side	..	1	8	14	..	..	..	..	..	9.57 ± .12		
Tanakius kitaharae												
Ocular side	..	..	11	98	63	11	1	..	..	10.42 ± .05	1.39	16
Blind side	..	..	14	104	60	6	..	..	..	10.32 ± .05		
Glyptocephalus stelleri												
Ocular side	..	..	..	13	14	11	2	..	..	11.05 ± .14	0.56	58
Blind side	..	..	..	9	25	5	1	..	..	10.95 ± .11		
Platichthys stellatus												
Ocular side	..	..	1	12	36	16	..	..	..	11.03 ± .09	3.83	0.01
Blind side	..	..	5	25	30	5	..	..	..	10.54 ± .09		
Kareius × *Platichthys* hybrids												
Ocular side	..	..	1	3	7	10	2	..	..	11.39 ± .21	2.06	4
Blind side	..	..	..	7	12	4	..	..	..	10.87 ± .14		
Kareius bicoloratus												
Ocular side	..	..	1	..	33	44	4	..	..	11.61 ± .07	2.80	0.5
Blind side	..	2	..	8	38	33	2	..	..	11.28 ± .09		

teen of the seventeen specimens at hand; in the other three the fin is slightly longer on the eyed side). In *Citharoides macrolepidotus*, another very primitive species (Hubbs, *In press*), the number of rays seems to average as high on the blind as on the eyed side, if, indeed, it is not higher. In this species the fin of the lower surface, though shorter, is broader and has heavier rays than the fin of the upper side.

Atheresthes, a pleuronectid genus with the left eye on the dorsal margin, and the only member of the subfamily Pleuronectinae with the primitive type of olfactory lamellae, gives a very slightly but not reliably higher average for the blind (left) side. In *Atheresthes*, which contrasts with *Psettodes* in this respect, the fin of the ocular side is much larger than that of the eyeless side. The number of rays is probably about equal on the two sides in both species of *Verasper* (the average is slightly higher on the eyed side in one species and on the blind side in the other). It is perhaps significant that all the species just mentioned are more or less pigmented on the blind side, which in most flounders is white. A few other species have the averages very close, but the great majority have more rays in the eyed-side pectoral than in the blind-side fin. In the Bothidae the dimorphism in ray number is roughly proportionate to the degree of bodily asymmetry: slight in the most symmetrical genus, *Paralichthys;* somewhat more marked in *Pseudorhombus;* striking in the more asymmetrical genera, such as *Arnoglossus* and *Laeops* (Table VI) and *Chascanopsetta* (Kuronuma, 1940 : 48). Among the Pleuronectidae the dimorphism in numbers is less markedly increased in the most asymmetrical representatives. In the sinistral flounders (Bothidae) the difference between the upper pectoral fin (in this family the left one) and the right pectoral is greater as a rule than that between the right — normally uppermost — and left fins in the dextral group (Pleuronectidae). This asymmetry may be correlated with the probably greater number of rays in the left pectoral fin of the ambidextrous *Psettodes*. In six of the nine bothids tabulated (and also in *Chascanopsetta lugubris*) the ray counts of the two pectoral fins are found to differ on the average by more than 1.00 ray; the greatest difference for any of the pleuronectids is 0.67 ray.

As would be expected from the detailed analyses on *Platichthys stellatus*, the invariably sinistral (reversed) Japanese races of this

species have on the average more rays in the left (upper) pectoral than in the fin of the right side. The difference (0.49) is a little greater than the average for the Japanese pleuronectids. About the same difference (0.52) exists between the ray counts of the eyed-side and blind-side pectorals in the *Kareius* × *Platichthys* hybrids, which are dextral and sinistral in approximately equal numbers (Hubbs and Kuronuma, 1942: 298–301). The only other reversed specimens treated in Table VI are one each of *Citharoides macrolepidotus* and *Tanakius kitaharae.*

In the cases which have just been cited the number of rays in the pectoral fin, the characteristic which corresponds in the fish most literally to handedness in man, is associated with the general asymmetry of the body. In a somewhat converse relation various bodily asymmetries in the fiddler crabs appear to be correlated with the right or left location of the larger cheliped (Duncker, 1903; 1904: 632–633; Ludwig, 1932: 6–8, 202–210). Such relations give credence to the theories that dominant handedness in man may be related to some other major asymmetry, at some phase of development. There are, however, facts that argue against the validity of various causal relations that have been propounded.

Asymmetries and Bilateral Variations in Essentially Symmetrical Fishes

Like vertebrates in general, fishes other than the flounders and the soles appear on superficial examination to be completely symmetrical about the sagittal axis, but closer scrutiny indicates that in many respects the two sides are not perfect mirror images of each other. Dissection discloses that there are many fundamental and almost invariably monomorphic asymmetries in the digestive and circulatory systems. With very rare reversals, either right or left directions are taken or flexures assumed by various embryonic processes. Such asymmetries in the adult and embryo are well known and have been treated at length by Ludwig (1932), who gives a plethora of references. They are considered here only incidentally, and only so far as they are related to more superficial asymmetries. Particular stress is laid on the differences between corresponding structures of the two sides in degree of development, as measured by the number of parts making up these organs. The numerical treatment simplifies the statistical analysis of the data.

BILATERAL VARIATION IN NUMBER OF RAYS IN THE LEFT AND RIGHT PECTORAL FINS OF *LEPTOCOTTUS ARMATUS*

Particular emphasis has been placed in the present study on the differences between the two pectoral fins in respect to the number of rays. Among the bilateral asymmetries of fishes this is the one that corresponds most closely to right-handedness and left-handedness in man.

Our attention was directed to this problem during an analysis of meristic variation in *Leptocottus armatus*, a marine cottid fish of western North America. We noted that, when the number of pec-

TABLE VII

ANALYSIS OF ASYMMETRY IN PECTORAL RAY COUNTS OF *LEPTOCOTTUS ARMATUS*

L indicates that the count is higher on the left side; *R*, that the right fin has the higher number of rays.

Analyses	*N*	*L*	*R*	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	100 *P*
Analysis by localities						
1. Sitkalidak Island, Alaska	174	10	19	17	66	14
2. Admiralty Island, Alaska	104	7	16	22	70	9
3. Puget Sound, Washington	245	13	37	20	74	0.1
4. Grays Harbor, Washington ...	103	3	13	16	81	2
5. Nestucca Bay, Oregon	136	6	18	18	75	3
6. Humboldt Bay, California	221	13	31	20	70	1
7. San Francisco Bay region	223	17	32	22	65	3
8. Elkhorn Slough, California* ..	145	8	25	23	76	0.5
9. Morro Bay, California	218	14	30	20	68	2
10. Near Santa Barbara, California	397	33	49	21	60	10
11. Anaheim Bay, California	109	7	25	29	78	0.3
12. Mission Bay, California	119	10	19	24	66	14
Analysis by subspecies						
1–7. *L. a. armatus*†	1,214	69	167	19	71	0.00
8. Intergrades*	145	8	25	23	76	0.5
9–12. *L. a. australis*‡	847	65	124	22	66	0.00
Grand total	2,206	142	316	21	69	0.00

* Including nineteen specimens from Monterey Bay at Monterey and three from Old Creek near Cayucos, California.

† Including eight specimens from Santa Cruz, California.

‡ Including four specimens from Lower California.

toral rays differs on the two sides, the count for the right fin is usually the higher (Table VII). This relation holds for all twelve localities, from each of which a large sample was studied. In about one specimen in four or five the counts are asymmetrical (the percentage of asymmetry varies from 16 to 29, and usually runs from 20 to 25). Among the asymmetrical specimens from 60 to 81 per cent are right-handed, in the sense that the right pectoral fin (corresponding to the hand) has more rays than the left fin. The differences are of probable to almost certain reliability; the odds of significance are at least 7 : 1, usually much higher. When the asymmetrical counts are summed up for the two subspecies, the probability that the indicated excess of right-handedness was caused by chance is seen by the χ^2 test to be less than 1 in 20,000.

As a question of methodology it should be noted that much more decisive results were obtained by applying the χ^2 test to the fifth part of the counts (those that are asymmetrical) than by following the customary method of using all the counts to analyze the difference between the means for the two sides. When the latter course is followed, the bilateral differences are obscured by the mass of symmetrical counts, and the P values are much higher, that is, less indicative of significance (Table VIII).

TABLE VIII

COMPARISON OF AVERAGE NUMBER OF PECTORAL RAYS IN *LEPTOCOTTUS ARMATUS*

	Specimens	Mean ± *SE*		Difference ($R - L$)	t	100 P
		Left fin (L)	Right fin (R)			
L. a. armatus						
Sitkalidak Island, Alaska	174	19.42 ± .04	19.47 ± .04	0.05	0.8	42
Admiralty Island, Alaska	104	19.20 ± .05	19.29 ± .05	0.09	1.3	19
Puget Sound, Washington	245	18.98 ± .03	19.08 ± .03	0.10	2.5	1
Grays Harbor, Washington	103	18.86 ± .05	18.96 ± .05	0.10	1.4	16
Nestucca Bay, Oregon	136	18.93 ± .04	19.01 ± .04	0.08	1.3	19
Humboldt Bay, California	221	18.91 ± .03	19.00 ± .03	0.09	2.2	3
San Pablo Bay, California	157	18.45 ± .05	18.54 ± .05	0.09	1.3	19
Intergrades						
Elkhorn Slough, California	125	18.35 ± .05	18.44 ± .05	0.09	1.3	19
L. a. australis						
Morro Bay, California	218	18.28 ± .03	18.35 ± .03	0.07	1.8	7
Near Santa Barbara, California .	397	18.37 ± .03	18.40 ± .03	0.03	0.7	48
Anaheim Bay, California	109	18.42 ± .06	18.59 ± .06	0.17	2.0	5
Totals and weighted means ..	1,864	18.72	18.80	0.08	..	..

Throughout its long coastal range *Leptocottus armatus* is clearly right-handed in the sense that the right fin usually has the larger number of rays when the number in the two fins is different. The significance of this relationship becomes clearer on further analysis.

The independent variation of the two pectorals in number of rays, leading to a higher number in one fin than the other, is partly counteracted by the tendency for the two fins to vary together in number of rays. The coefficients of correlation for the twelve localities vary from 0.56 to 0.73, with standard errors ranging from 0.03 to 0.06; for *Leptocottus armatus armatus*, $r = 0.61 \pm 0.05$; for *L. a. australis*, $r = 0.67 \pm 0.04$; for the species as a whole, $r = 0.63 \pm 0.05$. For all the coefficients the significance is below the 1 per cent ($P = 0.01$) level, indicating a highly reliable correlation.

When the number of pectoral rays is higher in one fin than in the opposite fin, the count in the first fin is usually higher than the mean value for both fins. In other words, in respect to the number of rays the two pectoral fins show a positive correlation between deviation from partner and deviation from mean. The pertinent coefficients of correlation range for the twelve localities from 0.37 to 0.60, with only one value above 0.48. The corresponding standard errors range from 0.03 to 0.06, and P is consistently below 0.01. For the northern and southern subspecies, respectively, $r = 0.44 \pm 0.05$ and 0.43 ± 0.04.

In counting the rays in hundreds of pectoral fins of *Leptocottus* it became evident that the lowermost ray in a given fin was usually short when the ray count was high, and that this ray was ordinarily long when the count was low. Consequently, to test this observation and to analyze the relationship the lowermost ray of each pectoral was measured in numerous specimens from five localities. The measurements were made to the nearest 0.1 mm. and converted into thousandths of the standard length of the fish. For each locality the inverse relationship between number of rays and length of lowest ray was reliably established (Table IX).

It would seem that the small ventralmost ray usually present in pectoral fins having a high number of rays might be given a lower numerical value (some fractional value) than is assigned to the larger corresponding ray usually occurring in fins with fewer rays. On this basis there would be less than 1.0 ray difference between

TABLE IX

RELATION BETWEEN NUMBER OF PECTORAL RAYS AND AVERAGE LENGTH OF LOWERMOST RAY IN FIVE SERIES OF *LEPTOCOTTUS ARMATUS*

The average lengths of the rays are expressed in thousandths of the standard length. The underlying values in parentheses represent the standard errors of these means and the number of lowermost rays measured for each fin with the given total number of rays.

	Number of rays in pectoral fin						
	15	16	17	18	19	20	21
Near Santa Barbara, California (168 specimens; M = 18.38)	69.0? (±?; 1)	.. ..	72.0 (±1.1; 22)	63.9 (±.6; 183)	54.2 (±.7; 128)	46.5? (±?; 2)	.. ..
Mission Bay, California (137 specimens; M = 18.79)	.. ..	.. ..	72.7? (±?; 3)	64.1 (±1.0; 66)	53.0 (±.6; 190)	46.9 (±2.0; 15)	.. ..
Grays Harbor, Washington (101 specimens; M = 18.91)	.. ..	.. ..	69.5? (±?; 2)	67.6 (±1.2; 33)	58.0 (±.7; 148)	45.0 (±1.0; 19)	.. ..
Nestucca Bay, Oregon (136 specimens; M = 18.97)	.. ..	.. ..	.. ..	64.8 (±1.1; 39)	56.0 (±.5; 202)	48.0 (±.9; 31)	.. ..
Sitkalidak Island, Alaska (91 specimens; M = 19.40)	.. ..	.. ..	.. ..	67.6? (±?; 5)	67.7 (±.8; 103)	55.4 (±.9; 77)	47.7? (±?; 3)

the two fins when, for example, the counts are 18 left and 19 right, for the eighteenth ray of the left fin is more of a ray than is the nineteenth element of the right fin. Convention and convenience demand that the rays be enumerated as whole numbers, but it is important to keep in mind that the classes of ray counts could be indefinitely divided, according to the degree of development of the last ray. Not only for the pectoral fins but also for many other meristic series we are finding that there are many gradations between the successive counts; that is, that there is no real distinction between continuous and discontinuous (or discrete) variations. We expect to deal with this problem in a separate paper. For the present it may suffice to state that the lowermost pectoral ray in *Leptocottus* varies from the merest rudiment to a large ray, providing all transitional conditions between successive counts (of 18 and 19, for example).

The degree of development of pectoral fins with any given ray count is best measured by the size of the lowermost ray. This ray

varies much more in length than any other one and is the only one that grades into a rudiment. It is presumably the last to be formed in ontogeny. It may be assumed that, when an embryonic fin is larger than usual, it will develop an extra ray at the lower edge. If the fin in the embryo is smaller than usual, the lowermost ray will presumably be the one that fails to form. A slight increase in fin size at the critical time of ray formation would leave room for only a minute ray; a larger increase would permit a larger ray to be developed at the lower fin margin. This reasoning is in line with the idea that meristic elements such as vertebrae, scales, and fin rays are laid down at a relatively constant distance apart, in absolute terms, and that the number of elements developed depends on the space available, up to the time when development stops. It is immaterial whether the elements are formed simultaneously in a given space or whether the formation of parts continues as the space for development increases. In either case the potentiality for segment formation eventually ceases, and thus fixes a limit to the space over which the segments may form, either on one occasion or over a period of time. The number of parts laid down will then be proportional to the available space. Such an explanation seems to hold for the number of scales that are formed over the body (Hubbs, 1941a; Neave, 1943 : 81–82) and is applicable to the determination of the number of elements in various meristic series (Hubbs, 1926b).

Although the discussion may be oversimplified, one may continue with the same line of reasoning, using a diagram (Fig. 1) to help visualize the relations which the size of the pectoral fin at the time when the formation of new rays at the ventral edge ceases bears to the number of pectoral rays and to the size of the lowest ray in each fin. Let 5 be the usual condition, representing a pectoral fin with 18 rays of which the eighteenth is of moderate size, but longer on the right than on the left side. Fins 4, 3, 2, and 1 on the right side represent successively smaller fins, in which room is left at the lower end first for a short ray 18, then for a very long ray 17 (since there is now no room for ray 18 to form), next for a rather long ray 17, and finally for a ray 17 of moderate length. Further steps in the same direction would yield a fin with only 16 rays. On the left side similar changes take place, but ray 18 drops out sooner. Fins 6, 7, 8, and 9 on the right side are progressively larger, and

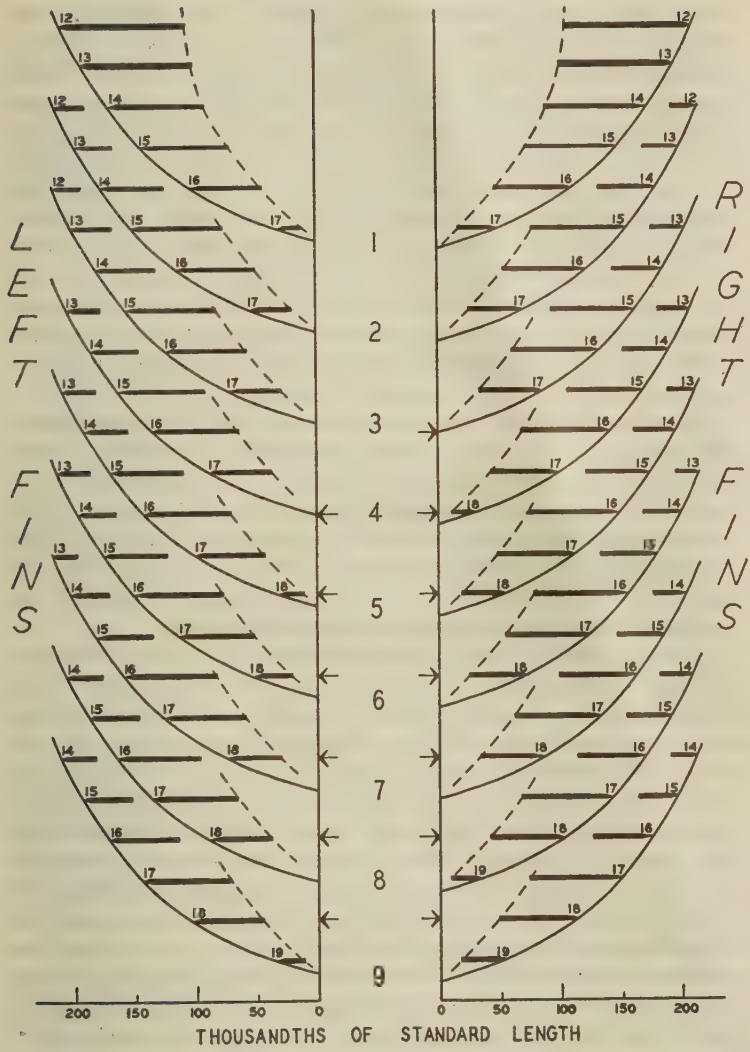

FIG. 1. Diagrams of lower portion of left and right pectoral fins of *Leptocottus armatus*, to illustrate the theory that the number of rays and the length of the lowermost ray are correlated with the size of the fin. The arrows point to the position of ray 18.

are characterized by an increasing length of the eighteenth ray; eventually there is added a nineteenth ray, at first small, then of moderate size. Further increases would allow for a still longer nineteenth ray and occasionally for yet another ray, giving a count of 20. On the left side similar changes again occur, but ray 19 is not added so soon. By the rule of normal variation fins of type 5 are most abundant, since this is taken as the mean condition, and the number of each type decreases in both directions. The diagram visualizes the lesser development of the left side, in terms both of average number of rays and of the size of the lowermost ray when the number is alike on the two sides. In the far north, where the pectoral rays are more numerous, the base of variation is shifted so that the nineteenth ray now replaces the eighteenth as the lowermost ray that is of moderate length (Table IX).

It seems clear that the number of rays in the pectoral fin is positively associated with sidedness, for the right fins have a higher average number of rays than the left fins. The interpretation has just been reached that the length of the lowermost pectoral ray is correlated positively with the total number of rays in the fin. When these relations were both determined, it was concluded that the size of the lowermost ray should differ in average length on the two sides, even when the ray counts are symmetrical.

It was observed that the fin which has the larger number of rays has the lowermost ray smaller than the corresponding ray of the opposite fin. Again following the reasoning illustrated by Figure 1 we conclude that the positive correlation between the two fins should render this relation almost invariable. When one fin (more commonly the right) is differentially enlarged sufficiently to introduce a new, short ray at the lower border, the opposite fin, with one ray fewer, should be somewhat enlarged, too, so that its last ray will be large. When one fin is differentially decreased just enough to eliminate a ray, the last ray becomes a large one; the other fin should be nearly as much reduced and should retain the extra ray, of a small size. The correlation was indeed found to be all but invariable in *Leptocottus* and almost as consistent in *Cottus bairdii* (p. 274). It was checked in 421 of the 458 specimens of *Leptocottus* that have asymmetrical pectoral ray counts. Of the 421 all but one had the lowermost ray the smaller in the fin having the higher count. In the one exception the last ray of the fin with

TABLE X

RELATIVE LENGTHS OF THE LOWERMOST RAY IN THE TWO PECTORAL FINS OF *LEPTOCOTTUS ARMATUS*

The consistent data for the five localities mentioned in Table IX have been combined. Specimens with no measured difference between the lengths of the lowermost ray of the two sides are equally apportioned among those having the ray longer on the left side and those having the ray longer on the right.

	Difference between lengths of lowermost pectoral rays of the two sides, in thousandths of the standard length									
	0	1–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33–36
Ray counts equal										
Ray longer in left fin ...	33.5	86	43	15	8	1	..	..	1	..
Ray longer in right fin ..	33.5	119	90	51	16	4	2	..	..	1
Left fin with more rays										
Ray longer in right fin ..	..	1	..	3	8	10	11	5	4	1
Right fin with more rays										
Ray longer in left fin ...	..	2	4	11	16	23	14	8	7	..
Ray longer in right fin ..	..	..	1	..	..	..	..	..	..	..

	Statistical calculations			
	Mean*	No. of specimens		100 *P*
		Δ = 0–4	Δ = 5–36	
Ray counts equal				
Ray longer in left fin ...	4.18	119.5	68	0.07†
Ray longer in right fin ..	5.58	152.5	164	
Left fin with more rays				
Ray longer in right fin ..	20.23	1	42	11§
Right fin with more rays .	18.01‡	2	84	
Ray longer in left fin ...	18.31	2	83	
Ray longer in right fin ..	7.0?	..	1	

* Means were derived from uncombined data.

† This 100 *P* value, derived from the χ^2 test, estimates the reliability of the distribution of the data according to whether the difference is none to slight (0–4) or moderate to large (5–36).

‡ In computing this mean the value of 7 (for the specimen with the longer owermost ray in a right pectoral with the higher ray count) is included as a minus figure.

§ This 100 *P* value estimates the reliability of the difference between the means, and is computed from the uncombined frequencies. In determining *t* and hence *P* the correction for diverse size of samples was used.

more rays (the right fin) was only 0.007 of the standard length longer than the corresponding ray of the left fin. The last pectoral ray averaged 0.019 of the standard length shorter in the fin with the higher number of rays, and was found to be more than 0.008 shorter in 118 out of 126 specimens (Table X). The difference in the length of the ray appears to be somewhat greater when the left fin has more rays than the right, presumably because the lowermost ray of the left fin has two reasons for being small: because it is in the fin with the higher ray count and because it is on the left side. The lowest ray of the right fin correspondingly has a double reason for being especially large: it is in the fin with the fewer rays and it is on the favored right side. The difference, however, is not of assured statistical reliability.

The most significant result obtained from measuring the length of the lowermost pectoral ray — the most sensitive criterion of the degree of development of the fin at the time the rays are formed — is the indication that on the average the right fin is the better developed even when the ray count is the same on the two fins. The evidence for right-handedness is, therefore, not limited to the fins with different ray counts, and the proportion of rights to lefts is greater than is indicated by the ray counts alone. The better development of the right fin is measured by the greater difference between the length of the last ray of this fin and that of the left fin, when the number of rays in the two fins is the same and when the lowermost ray of the right fin is the longer. The contrast is often striking. The moderate to large differences, of 5 to 36 thousandths of the standard length — those large enough to be observable and to be well beyond the error of measurement — are much more frequent when the right ray is the longer. When the left ray is the longer the difference is more often none to slight (0 to 4 thousandths of the standard length). The χ^2 test indicates that a very reliable distinction exists in the distribution of the data according to whether the difference in ray length for the two fins is none to slight, 0 to 4, or moderate to large, 5 to 36: $\chi^2 = 11.41$; $P = 0.0007$.

BILATERAL VARIATION IN NUMBER OF RAYS IN THE TWO PECTORAL FINS OF OTHER FISHES

After having found that the number of pectoral rays is higher on the right oftener than on the left side of *Leptocottus armatus*,

we turned our attention to published and original data on other fishes (Table XI), to learn whether what might be called right-handedness is of universal occurrence in fishes. The most pertinent published data were presented by the distinguished German student of variation Georg Duncker.

In a European percid, *Acerina cernua*, Duncker (1897 : 819, 830; 1900 : 359; 1904 : 560–562, 647, 651) found the asymmetrical counts to be divided nearly equally between lefts and rights. The ratios were 92 : 93 for 1,000 females and 65 : 49 for 650 males. He seemed to have some reliance on the indicated tendency toward sinistrality in the males, but Ludwig (1932 : 4–7), in reviewing the same data, regarded the counts as symmetrical. The χ^2 test indicates the difference to be wholly untrustworthy.

In one moderately adequate sample of another cottid, the European fresh-water *Cottus gobio*, results very much like those here given for *Leptocottus* were secured by Duncker (1897 : 830; 1904 : 567–568, 647, 652), who stated that dextrality was also evident in a smaller series (150 specimens) of the marine cottid *Myoxocephalus scorpius*. Duncker regarded the preponderance of higher ray counts in the right pectorals as significant, but Ludwig (1932 : 6), who arbitrarily fixed a limit of reliability at about 0.05 in Duncker's coefficient of asymmetry (see p. 232), regarded the fins of *Cottus gobio* as probably symmetrical. On the χ^2 test the difference (20 *L* : 42 *R*) appears trustworthy.

Duncker (1908 : 55, 103) discovered that at three localities the European pipefish *Syngnathus typhle* also has a higher count of rays in the right pectoral oftener than in the left fin.

Duncker's results, except for the neutral case of *Acerina*, thus stand in line with our findings on *Leptocottus*. To test this indication that fishes are predominantly right-handed in respect to the number of pectoral rays, new counts were taken on large series of two other species of the Cottidae, and pectoral ray counts of several species of cyprinodont and cyprinid fishes, previously made during other studies in our laboratory, were analyzed to see whether they, too, showed any significant bilateral asymmetry (Table XI).

The results for *Cottus bairdii bairdii* stand nicely in line with the data we secured on *Leptocottus armatus* and with those given by Duncker for *Cottus gobio*. The 1,372 specimens counted constituted a definite unit, for they were all taken in one poisoning of a

TABLE XI

BILATERAL VARIATION IN NUMBER OF RAYS IN THE TWO PECTORAL FINS OF VARIOUS FISHES

This table supplements Table VII. For source of data and other details refer to the accompanying text.

	N	L	R	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	$100\,P$
Cottidae						
Cottus bairdii bairdii	1,372	73	223	22	75	0.00*
Cottus gobio	354	20	42	18	68	0.5
Clinocottus analis australis	976	58	45	11	44	20
Syngnathidae						
Syngnathus typhle†	1,290	103	155	20	60	0.1
Percidae						
Acerina cernua	1,650	157	142	18	47	38
Cyprinodontidae						
Cyprinodon nevadensis	1,725	261	178	25	41	0.00
Oryzias latipes	368	74	44	32	37	0.6
Poeciliidae						
Mollienisia sphenops	743	74	63	18	46	35
Cyprinidae						
Siphateles, several forms	365	55	50	29	48	62

* A 100 P value of 0.00 indicates odds less than 1 in 20,000 that the result obtained is due to chance.

† The data are consistent for three localities.

spring pool on the grounds of the Wolf Lake Hatchery, Michigan. There were found 296 fish with the pectoral ray count different on the two sides, and of these the right count was the higher in 223; the left count, in only 73. The odds are much more than 1,000,000 to 1 against obtaining this difference by chance. The detailed statistical relations between the ray counts of the left and right fins of *Cottus bairdii* also agree beautifully with those for *Leptocottus armatus*. Thus the coefficient of correlation between the two counts is 0.64 ± 0.02. There is also a strong positive correlation between the deviation of each count from the mean and the deviation of the same enumeration from the count of the partner fin. The lowermost ray of the fin with the higher ray count is shorter than the corresponding element of the opposite fin in 288, or 97 per cent,

of the 296 specimens with asymmetrical counts (it was the longer in the eight other specimens). The mean for the left fin is 14.586, with standard error 0.0170; for the right fin, 14.696 ± 0.0166. The *t* value is 4.62 and the probability that the difference is due to chance is only 4 in 1,000,000. Thus, with sufficiently large samples (decreasing the standard errors), reliable indications of left–right asymmetry can be obtained by statistically comparing the means for the counts for the two sides.

The indication that the cottoid fishes are uniformly right-handed received a setback when the pectoral ray counts were made on 976 specimens of *Clinocottus analis australis*, collected on various dates in the tide pools of the adjacent headlands of Point Fermin and Whites Point, San Pedro, California. The ratio of lefts to rights in the 11 per cent of the specimens with asymmetrical counts proved to be 58 : 45. The chances are five to one that the left fin has on the average more rays than the right when the number differs on the two sides. The odds against *Clinocottus* being as strongly right-handed as *Leptocottus australis* or *Cottus bairdii* are almost infinitely large. How unsafe it is to generalize!

Slight to certain indications of sinistrality in the pectoral fins, as indicated by the number of rays, come also from counts of three cyprinodont fishes, and a bare suggestion of left-handedness is furnished by 105 counts for several forms of *Siphateles*, a genus of Cyprinidae from the American deserts (Table XI). The counts for *Cyprinodon nevadensis*, which were kindly made available by Robert R. Miller, pertain to various isolated subspecies living in the springs of the Death Valley region, California and Nevada. Virtually all the populations of the species are included in the data, and no indication was obtained that the races differ greatly in their tendency to be left-handed. The counts on *Oryzias latipes*, the *medaka* of the Japanese rice fields, were taken on series from many parts of Kyûshyû and Honshyû. Those for *Mollienisia sphenops* were made by Research Assistant W. Robert Martin on various subspecies from Guatemala and Mexico.

BILATERAL VARIATION IN NUMBER OF RAYS IN THE TWO PELVIC FINS

Moderately trustworthy figures indicate that the pelvic fin of *Leptocottus armatus* agrees with the pectoral fin in being better

developed on the right than on the left side (Table XII). The asymmetrical counts are so few, however, that separate analysis by localities is unwarranted. Out of a total of 3,208 specimens from all places only 58 had the count different on the two sides — 24 on

TABLE XII

BILATERAL VARIATION IN NUMBER OF RAYS IN THE TWO PELVIC FINS OF FISHES

For source of data and other details see text.

	N	L	R	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	$100\,P$
Leptocottus armatus						
All counts (*a*)	3,208	24	34	2	59	19
Inner ray rudimentary in opposite fin (*b*)	3,208	20	38	2	66	2
Sum, $a + b$	3,208	44	72	4	62	0.9
Cyprinodon nevadensis	1,821	313	280	33	47	18
Siphateles obesus pectinifer	409	43	15	14	26	0.02
Siphateles, several forms	1,884	182	112	16	38	0.00
Rhinichthys osculus	727	47	42	12	47	78

the left and 34 on the right. The greater weakness of the left side was better shown by the occasional rudimentation of the last ray. If we count this condition as R and the opposite situation as L, the ratio of variants is 20 L : 38 R. Combining the two sets, we find 44 sinistral to 72 dextral fish, in regard to the development of the pelvic fin. On this basis the distinction is rather trustworthy (see table). Usually there was no question whether or not the last ray was to be counted as rudimentary, for such a ray as a rule was very slender and was much less than half the length of the other rays. Often this ray could be detected only with good light and high magnification. A conscious effort was made to avoid the personal error of treating a ray as rudimentary in the left fin when a ray equally reduced was not so listed for the right fin. The recorded difference is thought attributable neither to chance nor to personal error. Somewhat figuratively we might speak of *Leptocottus armatus* as moderately right-footed.

Other fishes, however, are found to have the higher count oftener in the left pelvic than in the right fin (Table XII). This is almost

certainly true of the cyprinid fish *Siphateles*, as is indicated not only by the sum of counts of many series from different waters in the Great Basin, but also by the asymmetrical counts (43 lefts to 15 rights) among 409 additional enumerations for a single collection of *Siphateles obesus pectinifer* seined at one time along a beach of Walker Lake, Nevada. The results for the *Cyprinodon nevadensis* material (the same as that used for the pectoral counts) are by no means conclusive, but suggest that this species also may have the left pelvic fins slightly better developed than their right mates. No significant difference is indicated for *Rhinichthys osculus* (several subspecies).

The suckers (Catostomidae) show an unusually high percentage of bilateral asymmetry in the number of pelvic rays, and would therefore furnish excellent material to determine which fin, if either, more commonly has the higher count. Of 1,772 specimens counted 338, or 19 per cent, had the pelvic fins asymmetrical in the number of rays. Most of the counts, however, were made in other researches, and too few have been tabulated according to the side having the higher ray count to provide more than a hint that these fishes may also be slightly sinistral in respect to the pelvic fins.

In *Cyprinodon nevadensis*, which often lacks the pelvic fin on one or both sides (Miller, 1943 : 9–11), there is an indication of sinistrality, in the sense that the right fin seems to atrophy oftener than the left. Of 1,822 fish counted by Miller 112 (6 per cent) have one pelvic missing, and of these the fin is lacking on the left side in 47 specimens and on the right side in 65 ($\chi^2 = 2.91$; $P = 0.09$). In a race of wild carp (*Cyprinus carpio*) often lacking one or both pelvic fins Thompson and Adams (1936) found that the fin might be missing on either the left or the right side or on both sides, but they did not give the ratios.

ASSOCIATION BETWEEN ASYMMETRICAL DEVELOPMENT OF PECTORAL AND PELVIC FINS

Very little evidence is available to test the query, Is there an association between the better development, as measured by ray counts, of the pectoral and the pelvic fins? That is, to speak semi-figuratively, are right-handedness and right-footedness and left-handedness and left-footedness associated in the individual fish? The data for *Leptocottus armatus* and *Cyprinodon nevadensis* (Table

XIII) show no significant association, as measured by the χ^2 test. Fish with more right than left pectoral rays often have more left than right pelvic rays. As yet there is no reason to assume that any definite association or correlation exists between the differential bilateral development of the pectoral and the pelvic fins.

TABLE XIII

ASSOCIATION BETWEEN RIGHT–LEFT VARIATIONS IN NUMBER OF PECTORAL AND PELVIC RAYS

The counts were made by Carl L. Hubbs on 1,670 specimens of *Leptocottus armatus*, representing localities from Lower California to southwestern Alaska, and by Robert R. Miller on 1,724 specimens of *Cyprinodon nevadensis*, representing virtually all populations of this desert fish of the Death Valley region. For the counts of the *Cyprinodon* that are asymmetrical in both fins, $\chi^2 = 0.75$; the corresponding P value is 0.39.

	Count higher in		
	Left pectoral	Neither pectoral	Right pectoral
Leptocottus armatus			
Count higher in left pelvic	3	19	4
Count higher in neither pelvic	98	1,295	215
Count higher in right pelvic	1	30	5
Cyprinodon nevadensis			
Count higher in left pelvic	45	210	33
Count higher in neither pelvic	177	875	124
Count higher in right pelvic	39	200	21

BILATERAL ASYMMETRY AND VARIATION IN BRANCHIOSTEGAL CHARACTERS

Some of the most significant yet least noticed of the bilateral asymmetries of fishes relate to the branchiostegal membranes which enclose the branchial chamber ventrally on each side. In species having the two membranes separate that of one side overlaps the other. The overlapping member is the more ventral in position when the membranes are folded together. In some fishes the bony branchiostegal rays which support the soft tissues differ in number on the two sides.

Overlap of branchiostegal membranes. — It has already been noted (p. 244) that the few flounders with separate gill membranes follow

the general rule for fishes that the left membrane overlaps the right. This basic asymmetry has generally been overlooked, we believe, except in one paper (Hubbs, 1920). Observations made in connection with other researches, particularly a comparative study by Hubbs and Lagler (MS) on the gill structures of the clupeoid fishes, led us to conclude that the left branchiostegal membrane invariably folds over the right one in all fishes in which the membranes have not become united with each other or with the isthmus. This conclusion is now confirmed by a determination of the overlap relations of these tissues in ten specimens of the ladyfish, *Albula vulpes*, from various localities; in 476 young herring, *Clupea harengus*, from one series taken near Woods Hole; and in 183 fingerling king salmon, *Oncorhynchus tshawytscha*, from streams in Oregon, Washington, and Idaho (Table XIV).

As is true of almost all generalizations in biology, we now find,

TABLE XIV

BILATERAL ASYMMETRY AND VARIATION IN BRANCHIOSTEGAL CHARACTERS OF ESSENTIALLY SYMMETRICAL FISHES

For source of data and other details see text.

	N	L	R	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	$100\,P$
Overlap of branchiostegal membranes						
Albula vulpes	10	10	0	100	0	0.4
Clupea harengus	476	476	0	100	0	0.00
Oncorhynchus tshawytscha	183	183	0	100	0	0.00
Esox vermiculatus	442	410	32	100	7	0.00
Number of branchiostegal rays						
Left membrane overlapping right						
Albula vulpes	10	9	0	90	0	0.8
Oncorhynchus tshawytscha	46	37	0	80	0	0.00
Esox vermiculatus						
Posterior rays	410	28	58	21	67	0.1
Anterior rays	410	110	51	40	32	0.00
Total rays	410	88	52	34	37	0.2
Right membrane overlapping left						
Esox vermiculatus						
Posterior rays	32	1	1	6	50?	..
Anterior rays	32	3	9	37	75	15
Total rays	32	2	8	31	80	11

however, that in at least one species some exceptions to this rule occur. Among 442 specimens of *Esox vermiculatus* from southern Michigan, examined to determine the bilateral variation in the number of branchiostegal rays, 32 (7 per cent) have the right membrane external. It was a real surprise to note this variation in a character which has remained invariable, in regard to the typical condition, throughout the Holostei and the Teleostei. These data on the folding of the branchiostegal membranes emphasize both the fundamental nature of the left–right relationships in general and their susceptibility to reversal.

Because of the sharp compression of the head the membranes in the herring overlap throughout most of their length. Posteriorly the first three branchiostegals on the right side form a prominent shelf, the recess of which receives the adjacent edge of the left membrane. In this region, therefore, the left membrane overlaps the right one, but is in turn overlapped by a process from the right side.

Number of branchiostegal rays. — The rule that the left branchiostegal membrane overlaps the right led us to wonder whether this asymmetry might not be correlated with a bilateral difference in the number of branchiostegal rays. We had noticed for years that the number of these bony stays is often different on the two sides in certain fishes, particularly the Salmonidae (salmons and trouts) and the Esocidae (pikes), but we had made no tabulations to determine whether the counts average the higher on the left or on the right side.

Jordan and Evermann (1896 : 479) described the branchiostegals of the king salmon, *Oncorhynchus tshawytscha*, as "B. 15 or 16 to 18 or 19, the number on the two sides always unlike," but we know of no correlation of counts with the sides. Examining forty-six fingerlings of this species from Oregon and Washington, we find that the counts are alike on the two sides in 20 per cent of the fish, and that in the other 80 per cent the count is one or two higher on the left side than it is on the right (Table XIV). When the counts are symmetrical the last (anteriormost) ray is often reduced in size or even rudimentary on the right side. *Oncorhynchus tshawytscha* may therefore be classed as strongly sinistral in respect to the number of branchiostegal rays. In this species the left branchiostegal membrane consistently overlaps the right, but only for a short distance

anteriorly, since the two membranes diverge widely backward. In the region of overlap the anteriormost rays are the more deeply covered by tissue on the left side.

An even closer correlation between the character of the two branchiostegal membranes and the number of rays in these membranes seems to hold in the ladyfish, *Albula vulpes* (Table XIV). In this primitive clupeoid the left membrane not only overlaps the right membrane but is also much more expansive. In association with the greater available space the left rays outnumber the right by one or two in nine out of the ten specimens examined; in only one is the number equal on the two sides.

In *Esox vermiculatus* the membranes are subequal in size and the difference in number of rays on the two sides requires long statistical analysis for reliable demonstration (Table XIV). When, as is usual, the left membrane overlaps the right, the left branchiostegals on the average outnumber the right. This is not true, however, of the posterior rays, which are attached to the outer surface of the hyoid arch, behind the posterior insertion of the geniohyoid muscle. These outer, posterior, rays on the average are more numerous on the right side. The anterior rays, which are attached to the inner surface of the arch because they are overlain by the large *m. geniohyoideus*, have the average count definitely higher on the left side. In respect to the number of rays the posterior group of branchiostegals is dextral; the anterior group is strongly enough sinistral to render the total number slightly but significantly higher on the left side. This seeming contradiction finds a plausible explanation in the better average development of the geniohyoid muscle on the left side when the left membrane overlaps the right. The extent of this muscle is no doubt correlated with the number of anterior rays.

When the right branchiostegal membrane overlaps the left, as it does in 32 of the 442 specimens of *Esox vermiculatus* studied, the numerical relations of the branchiostegal rays seem also to be reversed (Table XIV). Now the anterior rays and the total rays on the right side appear to outnumber those on the left. Because of the small number of specimens the difference between the sides, though probable, is by no means certain. For the anterior rays and the total rays, however, the relative numbers of rights and lefts can be regarded as reliably different in the two lots (those with

the left membrane overlapping and those with the right membrane the more external); the probability of obtaining ratios of 110 : 51 and of 3 : 9 from two parts of a homogeneous series is about 2 in 1,000; the probability of getting counts of 88 : 52 and of 2 : 8 from two samples of a homogeneous whole is about 8 in 1,000. The direction of overlap of the membranes and the different muscular development along the hyoid arches of the two sides seem to be more significant than leftness or rightness as such, as a correlative of ray number.

Such bilateral differences in the number of branchiostegal rays will probably be found to occur in relatively few fishes. The acanthopterygian fishes and their relatives have a low number of branchiostegals (4 posterior + 0 to 4 anterior), and the number is often constant for species and even families (Hubbs, 1920). In many soft-rayed fishes also the number is constant within families (for example, three throughout the Cyprinidae and Catostomidae). Differences between the sides are to be looked for among those malacopterygian fishes which, like *Albula*, *Esox*, and the Salmonidae, have a high and variable number of branchiostegals.

It will be interesting to determine whether average differences exist between the numbers of gill rakers on the arches of the left and right sides. No pertinent counts seem to be available.

BILATERAL ASYMMETRY AND VARIATION IN OTHER CHARACTERS

The paired fins and the branchiostegal membranes and rays are by no means the only bilateral structures of fishes that may be differentially developed on the two sides. Several additional characters have been tested, and an indefinite number remain to be studied. The few analyses that have been made support the impression gained from systematic studies that the various bilateral organs are generally about equally developed on the two sides. The left and right elements of a few structures, however, differ markedly in average number or in other indices of relative development.

Scales and plates. — The only extensive comparison of the right and left scale counts on individual fishes which we have found is that by Voris (1899 : 236–237), whose data for the minnow *Hyborhynchus notatus* were reanalyzed by Duncker (1904 : 578, 647, 653) and Ludwig (1932 : 6). The difference between counts higher on the right

TABLE XV

BILATERAL VARIATION IN SCALE, GILL, AND TOOTH CHARACTERS AND IN MEASUREMENTS OF FISHES

For source of data and other details see text.

	N	L	R	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	$100\,P$
Lateral-line scales						
Hyborhynchus notatus	500	144	169	62	54	16
Plates along fin bases, *Zeus faber*						
Along dorsal base	250	68	76	58	53	50
Along anal base	250	65	61	50	48	72
Dorsal plus anal plates	250	79	79	63	50	100
Gill slits in hagfish						
Bdellostoma stouti	550	62	33	17	35	0.3
Teeth on rostrum, sawfishes						
Pristis, three or more species	84	20	28	57	58	31
Measurements, *Acerina cernua*						
Head length	692	76	60	20	44	16
Mandible length	692	86	103	27	54	21

side and those greater on the left is small and hardly of trustworthy significance (Table XV). For 600 specimens of *Percina caprodes* from Turkey Lake, Indiana, Moenkhaus (1895 : 282–283) gave an average of 89.46 for the left lateral-line count and of 89.74 for that of the right side, which, considering the number of specimens, would seem to be a significant difference, again favoring the right side. However, for 300 specimens for Tippecanoe Lake, Indiana, he gave a higher average for the left side (87.69 as compared with 87.45).

The modified scales that form the large plates along the dorsal and anal bases of *Zeus faber* differ in number somewhat oftener than not on the two sides (Table XV), but the counts are higher on the one side almost exactly as often as on the other. The data, from Byrne (1902), were also treated by Duncker (1904 : 564–567, 647, 652) and Ludwig (1932 : 6).

A nearly constant asymmetry in an epidermal plate in the desert tortoise, *Gopherus agassizii*, was mentioned by Grant (1936 : 225). He stated that the left gular plate is the better developed in 331 out of 366 specimens. This relation holds true in several specimens examined by Norman Hartweg and us.

Gill slits in hagfish. — One of the most noteworthy bilateral differences in countable characters, that of the number of external gill openings in *Polistotrema stouti*, escaped the notice of Ludwig (1932). The count is asymmetrical in about one sixth of the specimens, and in these the openings are more numerous on the left side nearly twice as often as on the right (Worthington, 1905 : 628–633; counts summarized and analyzed in our Table XV). The bilateral difference in number of gills was found to be somewhat less extreme, for the last or supernumerary opening in eleven fish was accompanied by a remarkedly reduced gill or by no gill.

Rostral teeth of sawfishes. — Bilateral variation occurs with very high frequency in the number of teeth along the two edges of the rostral blade of the sawfishes (genus *Pristis*). Out of 84 specimens of at least three species from various localities 48, or 57 per cent, had 1 to 3 teeth more on one side than the other (Table XV). The count was higher on the left in 20 and on the right in 28. The difference in laterality is not reliable ($P = 0.31$), and the data are vitiated by their diversity. Large series of counts for single species at one locality are needed. Some of our data were kindly furnished by Leonard P. Schultz and by J. L. Baughman.

Pharyngeal teeth of Cyprinidae. — In many minnows the pharyngeal teeth of the main row on the two arches slide together to form a cutting mechanism. In several European species the teeth mesh in such a way that the number is higher on one side, usually the left, than on the other (von Siebold, 1863 : 172, 189, 214, 223, 227, 232, 236). The preponderance of higher counts on the left varies considerably (Table XVI), and most species have the same number on both sides. *Tinca tinca* is said to have commonly four or five on either side (von Siebold, 1863 : 107). Subsequent discussions of bilateral asymmetry in cyprinid dentition, for example, those of von Martens (1896 : 10) and Ludwig (1932 : 230), are obviously based on von Siebold's account. The later authors compared the asymmetrical dentition of cyprinids with the similar arrangement of hinge teeth which occurs, with very uncommon reversals, in the shells of bivalve molluscs (for references and for data on the asymmetries in freshwater mussels see van der Schalie, 1936).

Like asymmetry has been found to characterize most, and probably all, American Cyprinidae (chiefly western) in which the pharyngeal teeth of the main row commonly vary from four to five.

TABLE XVI

BILATERAL ASYMMETRY IN NUMBER OF PHARYNGEAL TEETH IN CYPRINID FISHES

For source of data see text.

	N	L	R	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	$100\,P$
European species						
Hybrid, "*Abramidopsis Leuckartii*"	45	24	0	53	0	0.00
Leucaspius delineatus	36	31	0	86	0	0.00
Rutilus rutilus (4 races)	104	79	0	76	0	0.00
Telestes agassizii	72	33	2	49	6	0.00
Phoxinus phoxinus	51	45	2	92	4	0.00
Chondrostoma (3 species)	95	10	1	12	9	2
Western United States species						
Gila orcuttii (*a*)	40	38	0	95	0	0.00
Hybrids ($a \times b$)	40	31	1	80	3	0.00
Siphateles mohavensis (*b*)	40	10	0	25	0	0.4
Siphateles obesus obesus	47	33	0	70	0	0.00

As a general rule, to which individuals but not species form exceptions, the higher number is on the left side when the count is asymmetrical. Supporting statistical data are not available for most species, but have been given by Snyder (1917 : 62) for *Siphateles obesus obesus* and by Hubbs and Miller (1943 : 356) for *Gila orcuttii*, *Siphateles mohavensis*, and hybrids between these species. These data are also analyzed in Table XVI.

Crossing of optic nerves. — The left–right relations in the decussation of the optic nerves of flatfishes have already been referred to (pp. 234–236). Some families of flatfishes and all fishes of other orders have a dimorphic chiasma, for either the left or the right nerve may be the more dorsal in the chiasma (in the Pisces there is no intermingling of the fibers where the nerves cross). Parker's counts (1903 : 222–224) of one hundred specimens of each of ten species led him to conclude that there is no significant difference in the number of individuals with the left nerve or the right nerve the more dorsal. Larrabee's more intensive research (1906), however, proved that the right nerve of the brook trout (*Salvelinus fontinalis*) and the cod (*Gadus morhua*) is on top somewhat oftener than is the

left nerve. The differences, though proportionately small, are quite reliable statistically (Table XVII). The mathematical significance of the difference seems not to have been appreciated by Ludwig (1932 : 232–234). Whether the other species studied have the nerve of one side dorsal the more frequently cannot be stated with assurance, for one hundred counts of each are insufficient for the

TABLE XVII

Bilateral Variation in Location of Optic Nerves in Chiasma of Essentially Symmetrical Fishes

All data for *Salvelinus* and most of those for *Gadus* are from Larrabee (1906); all other material is from Parker (1903). Specimens with the left or the right nerve the more dorsal are listed under *L* or *R*, respectively.

	N	L	R	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	$100\,P$
Salvelinus fontinalis	4,642	2,057	2,585	100	56	0.00
Fundulus majalis	100	51	49	100	49	84
Menidia menidia notata	100	61	39	100	39	3
Poronotus triacanthus	100	53	47	100	47	55
Pomatomus saltatrix	100	43	57	100	57	16
Stenotomus chrysops	100	49	51	100	51	84
Tautogolabrus adspersus	100	43	57	100	57	16
Tautoga onitis	100	45	55	100	55	32
Prionotus carolinus	100	53	47	100	47	55
Gadus morhua	1,152	471	681	100	59	0.00
Melanogrammus aeglefinus	100	48	52	100	52	69

determination of this point. Larrabee demonstrated that no significant differences in the offspring resulted when specimens of brook trout and cod with the left and the right nerve the more dorsal were mated in different combinations. For this reason we have tabulated as a unit all of his data for each species.

Proportional measurements. — Little effort has been made to determine whether bilateral differences exist in the body dimensions of the essentially symmetrical fishes (constituting all groups other than the Heterosomata or flatfishes). The only thorough test of this sort relating to parts not known to be asymmetrical was made by Duncker (1900 : 562–564, 647, 651). His data, referring to the length of the head and of the mandible on the two sides of *Acerina cernua*, were reviewed by Ludwig (1932 : 6–7), who regarded these

parts as symmetrical. The measurements were probably not expressed very precisely, for the indicated percentage of asymmetry is only 20 and 27, respectively, for the head and the mandible. When the measurements were bilaterally asymmetrical the head was more frequently the longer on the left side, the mandible more frequently the longer on the right. The differences, however, prove on the χ^2 test to be of very low reliability (Table XV).

Significant differences between the relative lengths of the lowermost pectoral ray on the two sides have been demonstrated for cottoid fishes (pp. 266–272 and 274).

Coloration in a larval eel. — One interesting case of bilateral asymmetry in coloration has been recorded for a fish in which the body and eyes are symmetrical. The postlarvae of an eel, known as *Leptocephalus diptychus*, are marked on each side by a row of conspicuous spots, which alternate in position, though all are clearly seen from both sides of the transparent ribbon-like body. In both specimens the spots number three on the left side and four on the right (Eigenmann and Kennedy, 1901).

Association of Sex with Bilateral Asymmetries in Fishes

The question has arisen whether the left-and-right asymmetries of fishes are correlated in any way with sex. There is considerable evidence that the proportion of left-handedness differs in males and females of the human species (Ludwig, 1932; Wile, 1934). The published data are conflicting, and some workers claim that the apparently greater incidence of left-handedness in human males is the result of social factors. Ludwig, however, concluded (p. 311) that 4 to 5 per cent of human adult males are left-handed, and that the percentage is only about half as large in adult females.

The original data for pectoral rays in *Leptocottus armatus* and for pectoral and pelvic rays in *Cyprinodon nevadensis*, and Duncker's data for pectoral rays in *Acerina* and *Syngnathus* and for pectoral rays and three other characters in *Platichthys flesus*, all referred to previously, are available for a test of the association of sex with bilateral asymmetry in fishes (Table XVIII). The frequencies for the two sexes are not certainly different for any character, but give some evidence of being different, especially for the pectoral rays. In some species the males are indicated as possibly the more sinistral, in others the more dextral, in respect to number of pectoral rays.

TABLE XVIII

ASSOCIATION OF SEX WITH BILATERAL ASYMMETRIES IN FISHES

Counts higher on the left or the right side are listed under *L* or *R*, respectively. Significance of association is determined by the χ^2 test ($\chi = t$).

	N	*L*	*R*	*t*	100 *P*	Males *
Pectoral rays						
Leptocottus armatus						
Males	839	62	120	1.30	19	*L*
Females	814	40	106			
Acerina cernua						
Males	650	65	49	1.23	22	*L*
Females	1,000	92	93			
Syngnathus typhle						
Males	202	19	46	1.43	15	*R*
Females	362	31	45			
Cyprinodon nevadensis						
Males	857	132	102	1.48	14	*R*
Females	853	128	74			
Platichthys flesus (dextral)						
Total rays						
Males	562	5	351	1.93	5	*R*
Females	497	12	310			
Branched rays						
Males	528	2	516	1.36	17	*L*
Females	486	0	476			
Pelvic rays						
Cyprinodon nevadensis						
Males	888	146	130	0.42	67	*L*
Females	911	155	148			
Platichthys flesus (dextral)						
Total rays						
Males	559	6	19	1.22	22	*R*
Females	497	14	22			
Branched rays						
Males	558	17	222	0.28	78	*L*
Females	496	14	203			
Extent of lateral line						
Platichthys flesus (dextral)						
Males	480	71	141	0.94	35	*R*
Females	544	84	138			
Side bearing eyes						
Platichthys flesus						
Males	602	40	562	0.21	83	*L*
Females	518	20	498			

* In this column *L* indicates that the males appear to be more sinistral and *R* that they may be more dextral than the females in the given character.

This association of sinistrality and dextrality with sex, if it actually exists, is not related to the differential development of the fins in the species as a whole.

Sexual Rights and Lefts

In the literature on bilateral asymmetry reference has frequently been made to the "sexual rights and lefts" of *Anableps*. This is a genus of surface-swimming viviparous cyprinodont fishes still more famous for the division of the eye into two parts, one adapted for aerial vision and one for subaqueous vision.

These statements regarding sexual rights and lefts in *Anableps* rest on the accounts by Garman (1895a: 73–74, pl. 7; 1895b: 1012–1013, figs. 1–4). In monographing the Cyprinodontes this author discovered that the structure of the gonopodium (a highly modified anal fin) of *Anableps* adapts it more for sidewise than for vertical motion, and that this intromittent organ appears to be functionally effective toward the left in some males, toward the right in others. He also observed that the oviducal opening of the female is covered either by an enlarged scale (the "foricula"), which opens along either its left or right edge, or, in one species, by several scales which open on one side of a groove. Garman assumed that mating can occur only between dextral males and sinistral females and vice versa. This was a logical deduction but remains to be proved. The theory that the males always mate from one side only is hardly consistent with the equal development on the two sides of the spiny contact organs on the scales.

Garman stated that nearly three fifths of the males are dextral, and two fifths sinistral, whereas the females exhibit the reversed ratio (about three fifths sinistral and two fifths dextral). He thought that these ratios confirmed his theory that only rights can mate with lefts, and lefts with rights. Garman's data, however, were scarcely adequate. His ratio of counts of lefts to rights for the males was 6 : 11 for *Anableps anableps* and 8 : 14 for all three species; for the females, 34 : 21 for *A. anableps* and 36 : 23 for all species. In specimens at hand the left–right ratios are as follows: for *A. anableps* males, 0 : 1; for *A. dowei* males, 2 : 3; for *A. dowei* females, 3 : 1. These counts added to Garman's are analyzed for the three species combined (Table XIX). The deviation of the ratios from equality may be rated as probable but not dependable.

TABLE XIX

ANALYSIS OF SEXUAL LEFTS AND RIGHTS AMONG FISHES.

External structures only are considered. For source of data see text.

	N	L	R	$\frac{100\,(L+R)}{N}$	$\frac{100\,R}{L+R}$	$100\,P$
Genital opening on left (L) or right (R) side in *Anableps*						
Males	28	10	18	100	64	19
Females	63	39	24	100	38	9
Concavity on left (L) or right (R) side of gonopodium of males						
Poeciliopsis and *Poecilistes* (various species, Mexico and Guatemala)	400+	400+	0	100	0	0.00*
Allophallus kidderi	164	0	164	100	100	0.00
Unnamed genus, Guatemala	277	0	277	100	100	0.00
Xiphophorini (7 species)	365	182	183	100	50	100
Gambusia affinis affinis	353	179	174	100	49	84
Dermogenys pusillus	80	36	44	100	55	37
Location, left (L) or right (R), of aproctal side of males of Phallostethidae						
Phenacostethus smithi	334	155	179	100	54	19
Asymmetries in females of *Horaichthys*						
Location of genital pore, on midline or to left (L) or right (R) †	210	126	42	80	25	0.00
Presence of pelvic fins on both sides or only on left (L) or right (R)	210	205	0	98	0	0.00

* A 100 P value of 0.00 indicates that the odds are less than 1 in 20,000 that the result obtained is due to chance.

† Approximate figures, obtained from Kulkarni's statement that in about 210 females the genital pore was on the left side in about 60 per cent, on the right side in 20 per cent, and on the median line in the rest.

Naturally little significance can now be attributed to Garman's theory about the rôle of selection in the origin and in the possible future changes of these left–right relations in the sexes of *Anableps*.

Nor can much credence be placed in his theory (1896 : 232) that the sexual rights and lefts of *Anableps* were evolved to prevent close inbreeding between fish that swim habitually in pairs, side by side. In the first place, according to our observations, the various surface-swimming cyprinodonts commonly move in small groups, and there is no reason to believe that they pair off at any time other than when they are actually spawning. The idea that the pairs continually swim together seems to have stemmed from a fancy which Agassiz expressed when he applied the name *Zygonectes*, meaning "yoke swimmer," to the surface-swimming forms of *Fundulus*. In the second place, it is not to be expected that sibs would be any more uniformly rights or lefts than are more distant relatives. A more plausible theory is that the one-sided structure of the sex organs makes possible the completion of the copulatory act while the pair maintains the surface-swimming position for which *Anableps* is marvelously adapted. On the basis of recent work on sex recognition and breeding habits in fishes it seems probable that a male *Anableps* will attempt to mate with any other individual of the species, but will complete the act only with females and perhaps only with females having the opposite turn to the sex organs.

Garman's treatment of sexual rights and lefts in *Anableps* has been reviewed and discussed by numerous authors, including von Martens (1896 : 8–9), Meisenheimer (1921 : 166–167), and Ludwig (1932 : 230–231). Von Martens compared the two types of *Anableps* adults with the sexual rights and lefts of gastropods. Ludwig wrongly included *Zygonectes* among the South American genera in which the sperm duct penetrates the anal fin.

Garman wrote of "an allied genus of the family" in which the males only are modified into rights and lefts. He referred to *Jenynsia*, now classed in a separate family. Langer (1913 : 208–210) also discussed the question of rights and lefts in *Anableps* and *Jenynsia*, and stated that a male of *Jenynsia lineata*, which he observed, consistently mated to the right.

Sexual rights and lefts may also be distinguished among the Poeciliidae, the most speciose family of cyprinodont fishes. In some species we have noted that the fleshy structures connected with the oviducal openings are consistently directed toward one side. More definite bilateral asymmetries, in certain genera, characterize the gonopodium of the males (this is the intromittent organ, a modified

anal fin). In the Poeciliopsinae this structure is folded to form a tube along one side: on the left side in most genera; on the right side in *Allophallus* (and in another, unnamed genus from Guatemala); and on either side in *Xenophallus* (Hubbs, 1936 : 232–235). Statistical data have now been gathered to fortify these observations (Table XIX). Unfortunately, no adequate material is at hand by which to determine the ratio of rights to lefts for *Xenophallus*.

Sexual rights and lefts may also be distinguished among the poeciliid fishes in which the gonopodium is not folded to form a rigid tube. In the tribe Xiphophorini, for example, rays 3 and 5 of the anal fin in the adult male are more or less pulled toward each other to form a broad groove. As a result the deep trough of ray 5, along the fundamentally posterior edge of the gonopodium, is twisted toward the same side. The last anal rays are directed toward the opposite side. In this group as many males have the gonopodium concave on the left side as on the right. This was found to hold true for all seven species in the tribe, namely *Platypoecilus couchianus*, *P. xiphidium*, *P. variatus*, *P. maculatus*, *Xiphophorus montezumae*, *X. pygmaeus*, and *X. hellerii*. The consistent data for all the species were consolidated for presentation in Table XIX.

Gambusia, taken as an example of the many poeciliids which have the gonopodium proper rather rigidly fixed in one plane, is also indiscriminate in the laterality of the intromittent organ (Table XIX). In this genus only a trace of concavity is appreciable on either side of the gonopodium, but the short posterior rays are fluted, with the major concavity on either the left side or the right. In perhaps 10 per cent of the specimens examined the allocation into rights and lefts was more or less arbitrary, either because the concavity was very shallow or because of a doubly sigmoid curvature of the posterior rays.

Apparently the fixation of the concavity on one side of the gonopodium in the Poeciliidae was correlated with the elaboration of the trough into a definite tube.

There is some evidence to indicate that the poeciliids customarily copulate from one side. Philippi (1908 : 17) stated that among dozens of males of "*Glaridichthys januarius*" (= *Phalloceros caudimaculatus*) which he had observed all except four, which were reversed in this respect, swung the gonopodium to the left. Out of about twenty-five males of "*Glaridichthys decem-maculatus*" (= *Cnesterodon decem-*

maculatus) all copulated to the right, except three which moved the gonopodium to the left. Langer (1913 : 214) indicated that the morphology of the gonopodium made movement to the one side easier in these two poeciliids. Ludwig (1932 : 230–231), quoting Meisenheimer (1921 : 167) as a secondary authority, also stated that copulating usually to the left or to the right in these two cyprinodonts is correlated with the asymmetrical structure of the gonopodia. These organs in *Phalloceros* and *Cnesterodon* are nearly symmetrical and form no definite tube, but the posterior rays are curved to one side and movement of the sexual organ appears, at least in preserved specimens, to be easier toward one side (toward the right in the single male of each genus at hand). The indicated correlation between bilateral asymmetries in reproductive habits and in secondary sexual structures, in these and other viviparous cyprinodonts, calls for further inquiry.

Sexual rights and lefts also occur among the viviparous halfbeaks, Indo-Pacific fishes hitherto placed in the Hemiramphidae but more satisfactorily classed in a separate family, Dermogenyidae. In certain species of *Zenarchopterus* an enormously enlarged anal ray lies on either the left or the right side of the fin. In *Z. brevirostris* this ray lies to the left in three specimens, to the right in six (Mohr, 1926 : 253, fig. 15). In *Z. xiphophorus* it is on the left side of the fin in one fish, on the right in three (Mohr, 1934 : 11–12, fig. 2). We find that the rather elaborate gonopodium of *Dermogenys*, described in detail by Mohr (1936), is likewise either sinistral or dextral. On either the left or the right side the first three rays of the four-rayed gonopodium are folded to form a groove, which is partly enclosed by a fleshy process arising from the membrane between the third and the fourth rays. In eighty males of *Dermogenys pusillus* from various parts of Java, collected in 1929, the tube thus formed lies on the left side in thirty-six specimens and on the right in forty-four (Table XIX). The slight preponderance of dextral males in these data is not dependable statistically.

The males of the family Phallostethidae comprise individuals that are known to be rights and lefts in respect to mating behavior as well as structure. The complex clasping organ or priapium of these remarkable Asiatic fishes is asymmetrical in that, for example, the anus opens on the "proctal" side and the ctenactinia arise on the opposite or "aproctal" side. That the proctal and aproctal

sides are either right or left has been observed in all the main treatises on the phallostethids (Regan, 1916 : 5, 23; Myers, 1928 : 5; Villadolid and Manacop, 1934 : 200; Bailey, 1936 : 453; Aurich, 1937 : 264, 266, 275, 282; Herre, 1942 : 139). Villadolid and Manacop observed that a given male always clasps a female from the same side. Aurich showed for certain species that the asymmetry involves the rudimentary pelvics of the males, before these fins lose their obvious identity in the organization of the priapium. Since no statistical data have been published to itemize how "indiscriminate" the laterality of the priapium is, we have made counts of the side that is aproctal in 334 males of *Phenacostethus smithi* Myers, all collected by Hugh M. Smith at Bangkok, Siam (Thailand). This side was found to be left in 155 fish and right in 179 (Table XIX). The deviation from equality is not very reliably significant ($\chi^2 = 1.72$; $P = 0.2$).

In another bizarrely specialized Asiatic fish, *Horaichthys setnai*, bilateral asymmetries (Table XIX) are associated with clasping (Kulkarni, 1940). In this cyprinodont the females are usually lefts, in the sense that the oviduct opens to the left of the median ventral line in about 60 per cent of the individuals and to the right side in only 20 per cent (Kulkarni, 1940 : 401). A much more remarkable asymmetry in this fish is the almost invariable lack of the right pelvic fin in the female. Ordinarily, no trace could be found of either the right pelvic or its basal bone, at any stage of development. An adaptation seems to be involved (Hubbs, 1941b : 447), for the lack of the one fin provides the integumentary surface, opposite the oviduct, that is needed for the attachment of the spiny-headed spermatophore of this weird little fish.

Another very striking bilateral asymmetry associated with reproduction has been discovered recently in an unnamed cyprinodont genus from Guatemala. One of the several unique characteristics of this fish is the development on one side only of a structural complex to which a clasping function is obviously to be ascribed. The upper edge of the pectoral fin is transformed into an elaborate system of hooks and spines, and the scales on the base of the fin are enlarged and hardened to form a stiff plate with a free edge. In the single mature male collected it is the right fin that is so modified. The left pectoral is essentially normal, for it shows scarcely a trace of the bizarre specialization of the opposite member. Incidentally,

since Garman brought up the comparison, we might remark that in one respect this fish corresponds much more closely than *Anableps* with the fanciful *jaftak* of Persian literature, "a sort of bird that is said to have but one wing, on the opposite side to which the male has a hook, and the female a ring, so that when they fly they are fastened together." The female of the Guatemala poeciliid, however, shows no apparent modification which could be correlated with the clasping device of the male.

Bilateral Asymmetry of Rays

To some extent in many fishes, most notably in breeding males which have fins that are modified for clasping or copulation, the two halves of certain soft rays lose their complete bilateral symmetry. This is spectacularly true of cyprinid fishes, in which the pectoral fin of the breeding male is enlarged and thickened and bears nuptial tubercles on the inner surface. In *Rhinichthys atratulus*, for example, the basal part of the main pectoral rays is very different on the two sides. The upper hemitrichia (phyletically the left halves of the rays on the left fin and the right halves on the right fin), as compared with the lower hemitrichia, are ribbon-like instead of cylindrical, lack the posterior keel that is developed on the other side, have the segments fused farther outward, and have their origins much farther back along the base of the fin.

In adult males of *Gambusia* the "dorsal components" of rays three to five of the pectoral fin remain slender, while the "ventral components" of the same rays become greatly dilated (Turner, 1942 : 394). These components are the left and the right halves of the rays, but the bilateral relations have become reversed during the evolution of the fin. What is now the right, dorsal, inner face of the left fin was the left, outer, surface when the fin held its primordial fin-fold position. What is now the right half of each fin of the more advanced teleosts was originally the left side; what is now inner was then outer.

In the adult males of the Poeciliopsinae the detailed structure of the left and right elements of certain rays of the gonopodium are strikingly different (Hubbs, 1924 : 26, pl. 2; 1926a : 63, 68; 1936 : 233–235). In *Pamphorichthys minor* an even more remarkable bilateral asymmetry of a soft ray is manifested: on the left side the second pelvic ray retains the usual rodlike form, but on the right

side three subterminal segments are expanded into strong bispinous processes. This discovery was made by Luis Howell Rivero, whose unpublished drawing we reproduce, with thanks, as Figure 2.

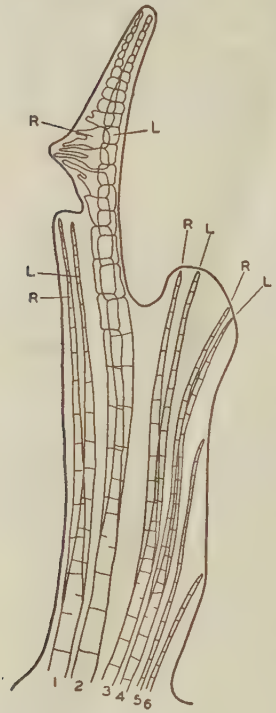

Fig. 2. Right pelvic fin of *Pamphorichthys minor*, showing the bilateral asymmetry of ray 2. Drawing by Luis Howell Rivero

The pectoral fins usually show some asymmetry between the left and right elements of each ray, particularly in the basal region of attachment, in correlation with the shift of the pectoral base from a longitudinal axis and ventral location to a vertical axis and lateral position. The outer and inner halves of the pectoral rays bear very different structural relations to the body. In the dorsal and anal fins the right and left sides of the spines (which, unlike the soft rays, are median unpaired structures) are somewhat dissimilar when the spines are heteracanthous, that is, when alternate spines are directed to right and to left. These asymmetries are not confined to breeding males.

Thus small parts of the body which have a bilaterally paired structure, or which merely have right and left sides, may develop bilateral asymmetry comparable to the dissimilarities between halves of the organism. When the bilaterally paired pectoral fins show such asymmetry within the ray structures, the direction of asymmetry is reversed on the two sides of the body, and each fin as a whole becomes the mirror image of the other. The spatial sequence of asymmetry is correlated with the general asymmetry of the fin, for the outer half of each ray differs from the inner half in the same way, whether either half be (fundamentally) left or right. This relation recalls the secondary asymmetries of the flatfish, in which the direction of asymmetry is correlated with the general asymmetry of the body, not with rightness or leftness as such.

General Interpretations and Conclusions

On the foregoing pages we have presented a considerable body of new evidence indicating that the right and the left sides of fishes are not exact mirror images of each other. Previous findings that point to the same conclusion are reviewed. Both the new and the old data have been subjected to statistical test, to appraise the trustworthiness of the information. Some suggestions have been made toward an explanation of certain of the observed differences between the sides. In the following sections the observations are further integrated, and the interpretations are brought to bear on certain problems of general biology.

Extent of Bilateral Asymmetries

Some degree of difference between the left and right elements of bilaterally paired structures may now be said to be of frequent occurrence among fishes. Particularly notable asymmetries, involving locomotion as well as structure, characterize the Cephalochordata — the highly modified derivatives of the ancestors of the fishes (Ludwig, 1932: 222–224). Marked differences between the sides occur in the gill region of the Marsipobranchii, which are at once the most primitive and among the most specialized of the fishes (p. 284 and Ludwig, 1932: 230). Among the more typical fishes many bilateral asymmetries occur, some of which are common to all the vertebrates (Ludwig, 1932: 224–228, figs. 109–110), whereas others are peculiar to fishes as a whole or to particular groups of fishes. The special asymmetries recorded through this treatise characterize many of the Pisces, both primitive and specialized.

The differences between the sides are best known and most strikingly displayed in the flatfish order (Heterosomata), but are by no means confined to that group. Some of the bilateral dissimilarities of the flatfishes are unrelated to the major asymmetry of the eyes and color, but numerous other differences between the sides are definitely correlated with the position of the eyes. Reversal of the sides involves only the latter set of asymmetries. Among the bilateral differences that are correlated with eyedness or blindness rather than with leftness or rightness as such are those that involve the number of rays in the paired fins. As a general rule, the fin of the blind side is the less developed.

Not only in the flatfish order but also among fishes in general bilateral asymmetries appear in all parts of the body, superficial as well as internal. Average differences between the paired fins, particularly as measured by the number of rays, seem to be frequent. Other asymmetries are exhibited in the folding of the branchiostegal membranes; in the number of branchiostegal rays; in the number of gill slits in a hagfish; in the teeth; in the crossing of the optic nerves; and in many other characters. Asymmetries in sexual structures produce sexual rights and lefts. Even fin rays may show differences between the left and the right rows of segments.

Bilateral differences thus characterize all groups of fishes and appear in many structures.

FACTORS DETERMINING BILATERAL ASYMMETRIES

Why the two sides of fishes differ from each other is a question which has never been adequately answered, and it seems doubtful that any simple, general explanation will be forthcoming. Some students of the problem have theorized that the asymmetries in the adult may be traced to a reversal of the flexure or the structure in the embryo or egg. The data on the flatfishes go far to negate this idea, for reversal of the eyes is correlated with only certain of the other bilateral differences — except in the single specimen which we interpret as completely reversed.

This lack of correlation between different asymmetries in the flatfishes and the independent manifestation of different asymmetries in teratological flatfishes which show a partial return toward symmetry are among the facts which lead us to conclude that a multitude of factors is involved in the asymmetry of the Heterosomata, and that the whole genetic and developmental mechanism has been keyed together to produce animals with sides as unlike as are those of the flounders. We think that this conclusion applies also to fishes other than the exceedingly asymmetrical Heterosomata.

The large degree of independence that seems to exist between the factors responsible for asymmetries in fishes may be regarded as an example of a general phenomenon. Simple cause-and-effect relations, particularly those that call for many consequences of some one developmental factor, are often easier to assume than to prove or confirm, and often fail to meet critical tests. Thus it has been proved by researches on dogs that the different symptoms of achon-

droplasia, though ordinarily associated with one another and related to the same endocrines, are caused in large part by independent genetic factors which are capable of being separated by appropriate genetic tests (Stockard, 1941).

That there is no consistent favoring of either the left or the right side is indicated by the facts: (1) that many structures show in different groups the same bilateral asymmetry, except for a 180° change in direction; (2) that many of the known asymmetries are subject to such reversal by individual variation; and (3) that individuals may be sinistral in some characters, dextral in others. Among individuals with a different ray count in the two pectoral fins the right count may be the higher more frequently in some species, the left count the higher more frequently in others. This contrast may even be shown by different species within one group. One family of flatfishes has the eyes and color on the left side, another is eyed and colored on the right side; and in each group individual reversals occur, rarely in most species but very commonly in others. There is little evidence of correlation between the sidedness of the pectoral and the pelvic fins.

In general, it appears to be of little concern to an animal whether the right side or the left side is better developed. As Sumner and Huestis (1921 : 445) have pointed out, structural changes in the anterior–posterior and the dorsal–ventral axes would seriously modify the environmental relations and welfare of an organism, but reversal in bilateral asymmetries has no such fundamental significance. It would appear that sinistrality and dextrality as such have little or no effect on an animal's chance for survival and reproduction. It is therefore easy to understand why, in respect to certain characters, some species are sinistral and others dextral, still others, either sinistral or dextral, in a 50 : 50 proportion or in any other ratio.

Asymmetry in itself, without reference to which side is favored, can often be interpreted with high plausibility as of adaptive value. Thus asymmetries in internal organs make for a division of labor between the sides. A flounder lying flat on one side is in a favorable position to simulate the bottom and thus to escape recognition and possible destruction.

Environmental factors related to the earth's rotation may have some effect on asymmetrical form and growth in plants, but they seem wholly unrelatable to bilateral asymmetries in free-swimming

animals. Little credence can be placed in the theories (for instance, those discussed, some with favor, by Wile, 1934) that sinistrality or dextrality in animals is due to such factors.

BEARING OF BILATERAL DIFFERENCES ON SYSTEMATICS

Since many superficial as well as internal characters are often more or less different on the two sides, it is obviously a wise policy in systematic studies to count or measure given characters consistently on one side, or to study both sides. The danger of inconsistent attention to the sides is perhaps greatest in racial studies. Thus, if in a research on the races of king salmon one investigator were to count the branchiostegal rays on the left side for certain localities and another (or the same) worker were to enumerate the rays of the right side for other localities, the sharp bilateral differences (p. 280) would likely be misinterpreted as characters of geographical races.

It remains to be determined whether direction and amount of asymmetry are consistent enough through series of species or groups to be usually indicative of phyletic relationship. Examples can be cited of such consistency, for instance, in the general pattern of visceral asymmetry of large groups. Whether the right or the left optic nerve is uppermost in the chiasma is a prime distinction between two families of flatfishes (p. 235). But whether in general the type of bilateral asymmetry of given structures is of systematic significance is an unanswered problem.

RELATION TO PROBLEM OF HANDEDNESS IN MAN

Many of the theories of handedness, reviewed at great length in such books as those by Parson (1924), Ludwig (1932), and Wile (1934), presuppose that this phenomenon is peculiar to man, or that handedness in man is unrelated to the observed bilateral asymmetries of other animals. The immense scattered literature on the subject is turgid with religion, mysticism, antique folklore, vaporous philosophy, Lamarckism, a plethora of mere argumentation, and an endless series of semiscientific ideas based on totally inadequate data. Most authors, even those with biological background, stress the ambidexterity of lower animals and apes and the imperfect development of right-handedness in primitive and degenerate men, and look on the elaboration of dextrality as an accompaniment of

progressive human evolution. Geneticists are flirting with the odd theory that left-handed humans are the survivors of identical twins, of which the dextral partner has failed to develop.

A consideration of bilateral asymmetries in the lower vertebrates, particularly the asymmetrical development of the forelimbs, helps to remove human handedness from its isolated position, and to integrate this phase of human biology with general biology. Some fishes which show bilateral asymmetry in the forelimb can be said to be right-handed, but even in these species many individuals have the left limb better developed than the right. Other species, however, may be said to be left-handed as a rule. Much of the discussion of factors determining bilateral asymmetries (pp. 298–300) applies to the problem of right-handedness.

In some flatfishes, as in man, handedness is correlated with modifications of the central nervous system, and handedness in fishes as well as in *Homo sapiens* is undoubtedly inherited. Whether or not man's ancestors were ambidextrous (a debated question), there is no good reason to assume that right-handedness in our species is a peculiar or an isolated phenomenon. No reliable evidence was obtained to indicate that sinistrality or dextrality in fishes is associated with sex.

An appreciation of the biological naturalness of handedness in man should help to dispel remaining traces of the primitive folklore which associates right-handedness with righteousness and left-handedness with the sinister. It should also help to exclude from the realm of serious consideration the not infrequently held misconception of handedness as a purely cultural expression.

The prevalence of right-handed and left-handed conditions among the fishes removes the necessity for explaining human handedness on a specifically human basis, but does not preclude the possibility that right-handedness in man arose as an adaptation connected with the handling of tools or the wielding of weapons. There is particular plausibility in the frequently proposed idea that holding the shield on the vital left side and wielding the spear by the strong right arm were basically correlated with the sharp differentiation between the arms of man. It seems unlikely that these customs initiated right-handedness; it is more probable that through natural selection the differentiation of the arms may have been intensified and rendered more nearly universal.

SUGGESTIONS FOR FURTHER RESEARCH

Several new lines of inquiry into the problem of laterality in fishes present themselves. An extensive statistical inquiry into the extent of the phenomenon is needed to understand the various correlations involved and to bring the data on asymmetry to bear on systematic problems. By focusing attention on the number of rays in the pectoral and pelvic fins, for example, we may learn whether dextrality and sinistrality are related to taxonomy, to shape or position of fin, to habitat, or to mode of life; whether symmetry or asymmetry is the usual condition; whether dextrality is more frequent than sinistrality in individuals and in species. Other lines of research are needed to determine whether locomotor or other functional asymmetries are involved.

By modern methods of physiological research it may be possible to determine whether there is a difference in the metabolic level of the two pectoral fins during the stage at which the number of fin rays and the relative length of the lowest ray are established. The oxidation-reduction pattern may be determinable by the vital stain method which has recently been used by Rulon (1935) and by Child (1942, 1943) in demonstrating the axial gradients in developing animals, including the fish *Oryzias*. In this way one might be able to test and analyze the correlations between differential metabolism and distinctive segment numbers, which have been suggested (as by Hubbs, 1926b) on largely theoretical grounds. The idea that available space is a main factor in determining the number of meristic elements (p. 268) can be put to test. In using paired structures of individual embryos or larvae one would largely eliminate many variables — such as the age, previous history, stage of development, and genetic constitution of the subject.

Perhaps sometime we shall learn by such studies why, for example, the pectoral fin in one race or species ordinarily forms fifteen rays, whereas this fin in a related kind of fish produces sixteen rays. An answer to this problem would materially advance our appreciation of the physiological fundamentals of speciation.

Summary

The left and the right halves of fishes are not perfect mirror images, for many of the organs are more or less unlike on the two

sides. Bilateral asymmetries affect all groups of fishes and appear in various organs, superficial as well as internal.

Duncker's index of asymmetry (α) confuses the amount and the direction of asymmetry. It seems better to express these factors separately, as the percentages of asymmetry and dextrality. The significance of the ratios of lefts and rights among the asymmetrical individuals is appraised by the χ^2 test, which leads to a probability estimate (P).

The outstandingly asymmetrical vertebrates are the flatfishes (Heterosomata). *Psettodes* is the only genus that is indiscriminately dextral or sinistral, on a primordial basis. Some families are normally dextral, others sinistral; one family has both dextral and sinistral genera. Reversal of sides is generally very rare, but is common in a few species, chiefly of the North Pacific. There is some evidence that reversal is accompanied by a decrease in viability. Reversed flounders are not true mirror images of normal individuals, for asymmetries of the optic nerves, viscera, and branchiostegal membranes remain unaltered. Only one specimen, newly discovered, seems to represent a complete change-over of the sides, presumably because of some basic reversal in the embryo or egg. Ambicoloration is regarded as a teratological return toward symmetry, in which various asymmetries are differently combined and therefore appear to be due to independent genetic factors. Most asymmetries in flatfishes are associated with the location of the eyes and color on one side. As a general rule, the pectoral fin of the eyed side, whether right or left, has on the average more rays than does the fin of the blind side.

Many bilateral asymmetries also characterize the essentially symmetrical fishes. Thus the pectoral and pelvic rays may be more numerous on the right side oftener than on the left. In other species the left fin is more frequently better developed when the two are unlike. The number of rays appears to be determined by the size of the fin when the formation of rays is completed. In general, the number of meristic parts in a structure probably depends on the space that is available at the time when the formation of the countable parts is completed. The length of the lowermost pectoral ray measures the degree of development of the fin. As yet there is no reason to assume that there is any positive correlation between the pectoral and the pelvic fin in regard to the direction of bilateral asymmetry.

With some reversals in *Esox*, the left branchiostegal membrane overlaps the right in fishes having these membranes separate. In *Albula*, *Oncorhynchus*, and *Esox* the branchiostegal rays in the left membrane more or less consistently outnumber those of the right. The trustworthiness of bilateral differences in the scale counts of fishes remains to be proved. In a hagfish the gill openings on the left side are more numerous oftener than are those on the right. In cyprinid fishes with asymmetrical dentition the larger number of pharyngeal teeth usually occurs on the left arch. In *Salvelinus* and *Gadus* the right optic nerve is the more dorsal in the chiasma slightly oftener than is the left nerve.

There is no clear-cut evidence that bilateral asymmetries in fishes are associated with sex. Sexual rights and lefts involving bilateral differences in reproductive structures and habits characterize several genera of fishes. Differences also occur between the two sides of certain soft rays.

A multitude of independent but usually associated factors appears to be responsible for bilateral asymmetries — an example of a general biological principle. Because of the average differences between the sides it is desirable in systematic and racial studies to make the counts consistently on one side or to study both sides. Some patterns of asymmetry are consistent enough to be of taxonomic value, but how generally the amount and direction of bilateral asymmetries can be used as systematic characters is not now apparent.

The frequent occurrence of bilateral differences between the forelimbs and between the left and right elements of many other structures of fishes counters the widespread idea that handedness is a peculiarly human trait, or the result of training.

It may be possible, particularly through physiological studies, to correlate the degree of development and the metabolic characteristics of the embryonic pectoral fin with the number of rays that are formed. Such investigations may materially advance our understanding of the physiological fundamentals of speciation.

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Head region of normal and totally reversed specimens of *Tanakius kitaharae*

Fig. 1. Normal (dextral) specimen, 210 mm. in standard length, from Sea of Japan

Fig. 2. Reversed (sinistral) specimen, 220 mm. long, from off Onahama, Japan

PHARYNGEAL POCKETS IN THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM* (LESUEUR) *

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INTRODUCTION

ALTHOUGH Hyrtl (1855, 1863) described and figured paired pharyngeal pockets in other clupeoid fishes, the present work is the first report of the occurrence of such structures in the gizzard shad, *Dorosoma cepedianum*. Their discovery in this fish was made by Kraatz while studying the food of the species in certain Ohio lakes. The descriptions by Hyrtl appear to constitute the only previous detailed research on these structures, which he called "*die accessorischen Kiemenorgane*" or "*die Kiemenschnecke*." Ridewood (1904) recognized their existence in his work on clupeoid osteology, and Bridge (1904) makes mention of them. Rauther (1910) summarized the occurrence of more or less comparable structures in the synbranchids, clupeoids, characinids, and other teleosts in his study of the accessory respiratory organs in bony fishes, but did little original work on the three families mentioned. We have examined several characins, however, and have failed to find the pockets.

It is the purpose of the present paper to describe the organ and to consider its possible function in the gizzard shad. Specimens examined and found to contain the structure were of both sexes and ranged in standard length from 18.8 to 261 mm.

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GROSS FEATURES

On raising the opercular bones on either side one may see the swelling of the lateral surface of the pharyngeal organ in the dorsal part of the area exposed (Pl. I, Fig. 1). It lies above the gills, just below the supratemporal and posttemporal and directly in front of the supracleithrum. The integument, which also covers the bones of the shoulder girdle, invests the structure laterally. Some musculariza tion of this superficial covering of the pockets is evident and may aid in their contraction.

The two pharyngeal pockets which compose the organ are paired; one lies on each side of the mid-line above the caudal part of the pharynx, but their mesial surfaces are not in contact with one another (Pl. I, Fig. 2). They are separated by a considerable space, which is only partly occupied by median and paired blood vessels. Each pocket constitutes an anteriorly extending diverticulum of the expanded chamber in the caudal roof of the pharynx, with which its lining is common and continuous. Innervation is by at least three principal branches of the vagus trunk on each side.

A more exact relation of the organ to the pharynx and to its supporting elements may be seen when it is viewed in parasagittal section, nearly midsagittal in position (Pl. I, Fig. 3). Posteriorly the pharynx extends dorsally and enlarges into a distinct chamber. The portals of the paired pouches and the esophagus lie near the highest level of this chamber, on approximately the same horizontal plane. The caudal opening into the esophagus is, of course, on the mid-line. The paired entries into the pharyngeal pockets are on either side and open cranially into the *entrance canals* of these structures.

Each pocket is chiefly supported by and attached to the greatly expanded epibranchial bone of the fourth gill arch, upon which it rests. The expansion takes the form of a lateral wing with lattice-like structure (Pl. II, Fig. 4; Text Fig. 1). Additional support and place for muscular attachment for the pharyngeal pocket are provided by a cartilaginous extension, which arises on the lateral edge of the

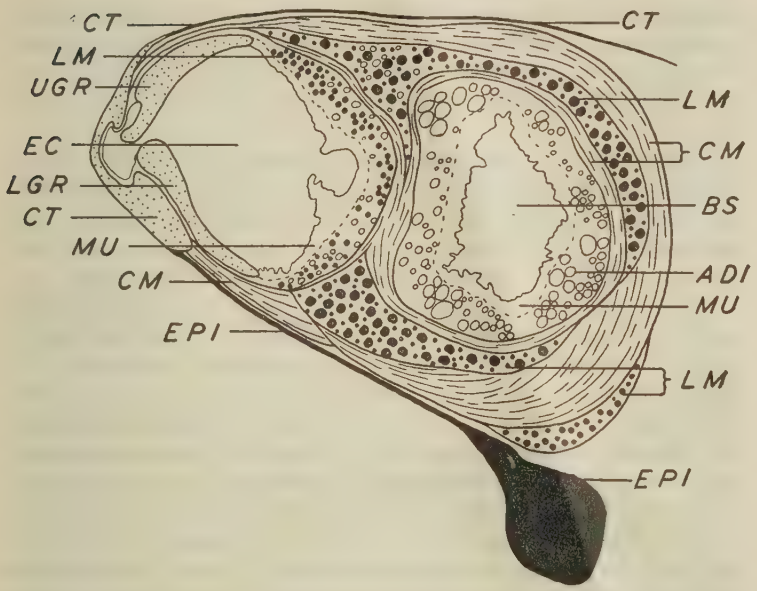

FIG. 1. Diagrammatic cross section of left pharyngeal organ of gizzard shad, viewed from behind. ADI, adipose and areolar connective tissue layer; BS, lumen of blind sac; CM, circular muscle bundles; CT, cartilaginous extension of epibranchial bone; EC, lumen of entrance canal; EPI, fourth epibranchial bone with lateral expansion; LGR, lower row of gill rakers in entrance canal (posterior row of fourth gill arch); LM, longitudinal muscle bundles; MU, mucosa and submucosa; UGR, upper row of gill rakers in entrance canal (anterior row of fifth pharyngeal arch). The magnification is about 8.9 diameters

bony expansion of the epibranchial. The cartilage exceeds the bone in area, and partly encapsulates the organ laterally (Pl. I, Fig. 2). Dorsally the cartilage leaves the organ and rises to terminate at the ventrolateral edge of the vertebral column. Its attachment to the vertebrae and adjacent body wall is by loose fasciae. The organ also lies somewhat upon dorsal branchial elements of other arches anteriorly and has some loose membranous attachment to the cranial base. This attachment is particularly to the region of the epiotics and to the keel-like ventral extension of the parasphenoid. The posteriorly directed angle and cartilaginous joint between the ceratobranchial and epibranchial of the fourth arch are supported by an

articulation with the dorsal prominence of the fifth ceratobranchial (the lower pharyngeal bone), which alone represents the fifth branchial arch on each side (Pl. II, Fig. 4). This support of the fourth arch by the fifth is similar to that in other clupeids as shown by Ridewood (1904).

The supporting mechanism is strengthened by the lower pharyngeal bones of the fourth arch. The single bone on each side is moderately strong and gives off both anterior and posterior processes near the mid-line. These processes augment the articular surface with the posterior median ventral cartilage of the branchial basket.

Each half of the organ is shaped roughly like an enlarged fish-hook (or a letter J) lying horizontally in the fish, with the "shank" lateral to the recurved, mesial, anterior terminal portion (Pl. II, Fig. 5), which forms a blind pouch. This sac has a greatly restricted lumen and a very thick wall of both muscular and adipose tissue. In these respects it is structurally unlike the entrance canal (the shank), which leads into it from the dorsal chamber of the pharynx.

Each entrance passage is equipped with two rows of gill rakers. These rakers, like those in the branchial chamber (Pl. II, Fig. 5; Text Fig. 1), are exceedingly numerous and close-set, but they are highly modified in that they are attached along most of one side and lack a denticulate margin. One of these rows is ventral, the other is dorsal; they extend laterally from near the middorsal and midventral lines of the canal respectively and have single free tips, reaching almost to the lateral wall. Here the terminations of the rakers of one series interdigitate with those of the other. Laterad to these interposed tips there is a smaller elongated chamber which is essentially blind at both ends, tapering till it disappears at its anterior and posterior extremities. The dorsal row is continuous through a reduced group of rakers in the dorsal wall of the pharynx with those borne by the fifth ceratobranchial. This row in the canal has a position similar to that which would be carried by a fifth epibranchial, were that bone present. The ventral row lies on the fourth epibranchial bone, for the most part, and is similarly continuous, by reduced rakers, with the typical rakers borne on the posterior (mesial) surface of the ceratobranchial of the fourth arch. The ventral row in the canal is thus obviously the same as the series of rakers normally borne on the posterior margin of the fourth epibranchial in fishes lacking the pharyngeal pouch. This more primitive

arrangement is retained on the third epibranchial in *Dorosoma* (Pl. II, Fig. 6) and on the third and fourth epibranchials of *Clupea*, as shown below in detail. The raker rows terminate anteriorly in the gizzard shad at the sharp angle where the canal connects with the blind pouch (Pl. II, Fig. 5).

The direction and extent of specialization of the pharyngeal structures in the gizzard shad may be shown by comparison with a more generalized clupeid, the Pacific herring (*Clupea pallasii*). For this purpose the following specimens were used: (1) *Clupea pallasii*, 182 mm. in standard length, U. M. M. Z. Cat. No. 61129; (2) *Dorosoma cepedianum*, 188 mm. in standard length.

Dorosoma shows a consistent tendency toward increased extension of gill filaments and augmentation of the number of gill rakers. The single row of hyoidean pseudobranch filaments is well developed in both fishes but numbers only nineteen in the Pacific herring, whereas in the gizzard shad there are thirty-one, all rudiments counted. The gills of the first three branchial arches are similar in both species except that in the gizzard shad there is a greater development in the group which arises from the anterodorsal extremity of each of these arches. In the fourth arch the filaments of the lower limb (below the angle between the epibranchial and the ceratobranchial) in both fishes are like those of the same region on the first three arches. On the upper limb of this arch in *Clupea* the double row persists until the most anterior ten filaments are reached. Here the posterior (inner) row (demibranch) ceases, and the ten remaining ones continue the outer row in single file. In *Dorosoma* the posterior row of filaments drops out much sooner after rounding the angle between the upper and the lower limbs. Only twelve pairs are in double series on the upper limb. The remainder continue the outer row to the farthest forward dorsal extremity of this fourth arch and are single. The location of this series of filaments is, however, much different from that in the Pacific herring. In the gizzard shad the row is near the lateral edge of the wing of the epibranchial, but in *Clupea* it is hardly displaced from the normal position along the body of the bone which, in this fish, lacks the winglike expansion.

The distribution of the gill rakers is fundamentally the same in *Clupea* and *Dorosoma*, although their kinds, number, and extent are different. Raker rows are developed in both as follows: on the anterior (lateral, outer) surface of both limbs of all five arches and

also on the posterior (mesial, inner) surface of the upper limb of arch three and the upper and lower limbs of arch four (Table I).

TABLE I

DISTRIBUTION OF GILL-RAKER ROWS IN *DOROSOMA* AND *CLUPEA*

Branchial arch	I	II	III	IV	V
Upper limb	1	1	2	2	1
Lower limb	1	1	1	2	1

The typical rakers of *Clupea* are rather uniformly attenuate, tapering only very gradually to a distal point. Each is somewhat laterally compressed and bears two rows of distinct teeth, one on each side. The rakers of *Dorosoma* are more strongly compressed from side to side but possess only very weak denticulations in a single row. Normally each raker is truncate and slightly enlarged distally after a constriction between the tip and the more lamellar base. All the rakers in the herring are similar to the single typical kind described and are stouter than those in the gizzard shad. Those of *Dorosoma*, however, are of two principal kinds. On an ordinary arch segment, such as the upper limb of the first, one out of every three to six rakers has a lappet-like expansion at its base; the intervening rakers lack this expansion.

The great difference in raker numbers between the herring and the gizzard shad is exemplified in the total raker count of the first arch; *Clupea* has sixty-seven, all rudiments included, and *Dorosoma* has more than three hundred (Hubbs and Whitlock, 1929). A similarly larger number is evident on all succeeding arches for the gizzard shad. Augmentation in total number of rakers is also accomplished in this species by great anterior extension of the posterior row of the fourth arch and of the row of the fifth arch. Apparently these two rows have secondarily become encapsulated in the pharyngeal pockets previously described. The corresponding dorsal rows are barely expressed in *Clupea;* the reduced rakers in both the posterior dorsal fourth row and the dorsal fifth row number only five. The total rakers within the pharynx of *Dorosoma* are so numerous and close-set that they obscure all the underlying structures. This is not so in *Clupea*, in which branchial arches and portions of the

pharyngeal floor and roof are not covered by rakers, which thus exposes other structures between them. In a contracted pharynx no spaces are visible to the naked eye between the rakers of *Dorosoma*, and it is only by riffling them that one may discern their individuality. Some increase in raker number is also attained by the continuity of all raker rows of one side with those of the opposite side. In the anterior floor of the pharynx this brings about a much closer encroachment upon the entoglossal in *Dorosoma* than in *Clupea*. In the anterior roof of the pharynx the gizzard shad has a well-developed free median cartilage, which supports the rakers of the first row where they meet on the mid-line and thereby increases their extent. The cartilage is attached posteriorly to the cartilaginous union of the pharyngobranchials of the first branchial arch and is lacking in the Pacific herring.

HISTOLOGICAL FEATURES

Description of histological features of the pharyngeal pockets is based on cross sections taken from approximately the middle of their length, cut ten to twelve microns thick, stained with hematoxylin and eosin, and mounted in clarite (Text Fig. 1).

The entrance canal is lined with a stratified squamous epithelium, which is neither glandular nor vascularized. The cartilaginous skeleton of each raker is covered with similar epithelium. Successive layers forming the mesial wall of the entrance canal are: (1) epithelium; (2) submucosa; (3) scattered longitudinal muscle bundles in areolar and adipose connective tissue; (4) thin stratum of circular muscle which is contiguous to a similar musculature surrounding the blind sac. Outside this circular muscle layer, and above and below part of the entrance canal, as well as in all of the wall between it and the sac and over most of the sac, there is more or less compact longitudinal muscle.

The blind sac is also lined with stratified squamous epithelium backed by submucosa of varying thickness. Outside these tissues there is a very thick zone of loose connective tissue, principally adipose. There follow the thin circular muscle layer previously mentioned, the longitudinal bundles, and, finally, the strong circular muscles that extend laterad above and below both sac and canal to insert principally on the cartilaginous capsule. The cartilage is thickened to receive these insertions. A small bundle of longitudinal

muscle is isolated on the ventromesial surface of the organ, lying just over the body of the epibranchial bone.

DISCUSSION AND CONCLUSIONS

No definite decision in regard to the function of the pharyngeal pockets in the gizzard shad has been reached. Earlier workers, notably Hyrtl (1855, 1863) and Rauther (1910), have interpreted similar structures in related fishes as of respiratory significance. The pharyngeal pockets of *Dorosoma* do agree in general location, at least, with the accessory respiratory organs of certain tropical fresh-water fishes (Rauther, 1910; Carter and Beadle, 1931), but are probably neither homologous with nor analogous to those organs. These structures in the gizzard shad are very similar to the branchial organs of other clupeoids as described by Hyrtl (1855, 1863), but whether they are of common origin and of similar function remains to be determined. It seems highly probable that Hyrtl erred in attributing a respiratory function to the pharyngeal pockets of clupeoid fishes.

Evidences that the organs in the gizzard shad are accessory to the digestive rather than to the respiratory system are as follows: (1) The epithelial lining of the lumen is stratified and nonvascular;[1] (2) The musculature is striated, indicating a voluntary control; (3) The included lamellar structures are modified rakers with a hard skeleton, not modified gill filaments; (4) The manner in which the organs may be accessory to the digestive system can be postulated on the basis of the structure and location of the organs and on the apparent needs of the fish. The extremely fine, numerous, and close-set condition of the gill rakers doubtless greatly impedes the passage of water. This circumstance may well create a requirement for extra pressure on the water in the pharynx, greater than that needed for expiration in fishes with more ordinary rakers. The extra pressure, partly in the form of an auxiliary head of water, could be provided by the constriction of the pockets and the expulsion of their contents simultaneously with contraction of the pharynx as a whole. With the next inflow of a respiratory current food concentrated on the rakers could then be carried into the expanded

[1] The "flagellated" border on the lining cells reported by Hyrtl (1863) for *Chanos* was not evident in our gizzard-shad material, which, however, was not specially preserved for histological purposes.

dorsal pharyngeal chamber and swallowed. Concentration of the food for swallowing could be due to the nature of the current (possible special turbulence) set up in the chamber or it might be associated with the stricture of the pockets. It seems likely that confusion of water currents, at the level of the esophageal opening, would concentrate foods insufficiently unless such an expanded chamber were present and unless water could pass anteriorly into the pouches. Since the esophagus has an unrestricted opening into the pneumatic duct, it seems unlikely that the pouches serve a function of forcing strained materials into this organ. Any great pressure in the esophagus would push food into the pneumatic duct to the swim bladder.

The possibility of a sensory function, perhaps for the recognition of plankton swarms, is admitted and would account for the conspicuous innervation by the vagus. Hyrtl (1863) concluded that this was the explanation for the richly innervated organ in the osteoglossid *Heterotis niloticus*, where branches of the vagus are distributed to the mucosa.

The obvious anterior sphincter-like constriction of the esophagus at its point of entry into the dorsal pharyngeal chamber must bear some relation to the process of swallowing, but the exact nature of its significance is obscure. Similarly, the reason for the departure of the esophagus from the more usual kind is not clear. In *Dorosoma* its walls are thin and smooth, being quite incapable of much stretching. In *Clupea*, a more generalized clupeid, the anterior part of the esophagus is thick-walled and, although slightly constricted, is beset with numerous villose rugae; posteriorly, too, it is thicker than that in the gizzard shad and is apparently more capable of stretching.

The foregoing comparison seems to indicate that the development of the pharyngeal pockets, with their contained rakers, is, at least indirectly, associated with an increase in the number of gill rakers. This indication supports our contention that the pouches are accessory to the digestive system and not to the respiratory one.

SUMMARY

1. Paired pharyngeal pockets constituting an organ associated with the upper limb of the fourth branchial arch and containing two rows of gill rakers are described in the gizzard shad.

2. The organ is lacking in a more generalized clupeid, the Pacific herring.

3. Evolution appears to be the result of an increased number of gill rakers.

4. Function is not respiratory but is accessory to that of the digestive tract.

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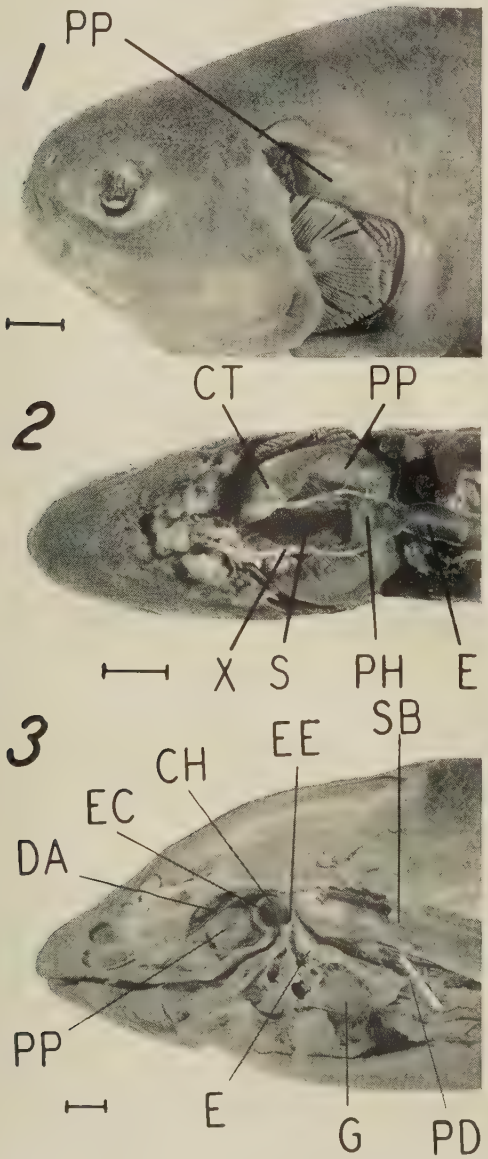
EXPLANATION OF PLATE I

(The scale bar equivalent is one centimeter.)

Fig. 1. Gizzard shad with opercle and preopercle removed to show lateral surface of pharyngeal pocket (PP) *in situ*. Adult female, 261 mm. in standard length, Grassy Pond, Gibson County, Indiana, summer, 1940

Fig. 2. Pharyngeal pockets (PP) of gizzard shad exposed from above. CT, cartilaginous extension of fourth epibranchial bone; E, esophagus; PH, roof of pharynx; S, space between pharyngeal organs; X, innervation by vagus nerve. Adult male, 224 mm. in standard length, Grassy Pond, Gibson County, Indiana, summer, 1940

Fig. 3. Parasagittal section of anterior portion of gizzard shad. CH, chamber resulting from dorsal expansion of pharynx; DA, dorsal aorta; E, esophagus with thin wall; EC, opening of entrance canal of right pharyngeal pocket into chamber; EE, point of exit of esophagus from pharyngeal chamber; G, gizzard; PD, pneumatic duct from esophagus to swim bladder; PP, mesial surface of right pharyngeal pocket; SB, swim bladder. Adult female, 249 mm. in standard length, Grassy Pond, Gibson County, Indiana, summer, 1940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EXPLANATION OF PLATE II

(The scale bar equivalent is one centimeter.)

FIG. 4. Alizarin preparation of branchial bones of gizzard shad for reference to the modification of the fourth epibranchials for support of the pharyngeal pockets. There are shown a dorsal view of the lower bones (A) and a ventral view of the upper bones (B), 1.25 times actual size. HY, Hyoid arch; I, first branchial arch; II, second branchial arch; III, third branchial arch; IV, fourth branchial arch; V, fifth branchial arch (ceratobranchial); EPI, epibranchial bone of fourth gill arch — extent of reflected cartilaginous expansion indicated by dashed line. Male specimen, 172 mm. in standard length, taken in Lake Erie, vicinity of Put-in-Bay, Ohio, October, 1943

FIG. 5. Frontal sections of pharyngeal pockets and dorsal chamber of pharynx, showing structure of pockets and relation to opening of esophagus. A, ventral section viewed from above; B, dorsal section viewed from below; ACV, anterior cardinal vein (?); AGR, anterior limit of gill raker rows in entrance canal; BS, blind sac; DA, dorsal aorta; E, esophagus with thin wall; EC, opening of entrance canal of right pharyngeal pocket into chamber; EE, entrance to esophagus; LGR, lower row of rakers; PH, roof of pharynx; UGR, upper row of rakers

FIG. 6. Roof of pharynx exposed and dissected by removal of arches two and three on right side of fish. I–IV, upper limbs of gill arches one through four; E, esophagus; EC, pointer into entrance canal of right pharyngeal pocket; EPI, epibranchial of fourth gill arch with pharyngeal pocket on its dorsal surface; GR, gill rakers; PP, ventrolateral surface of right pharyngeal pocket covered by expansion of fourth epibranchial

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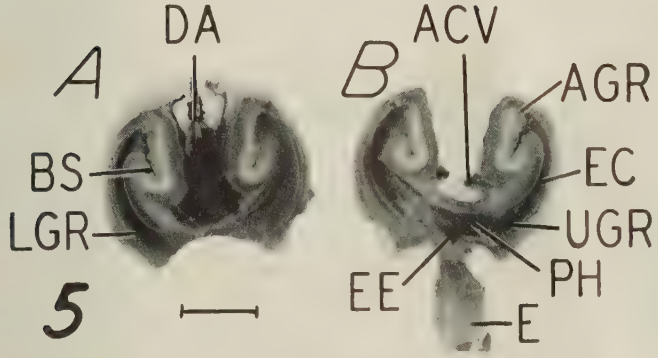
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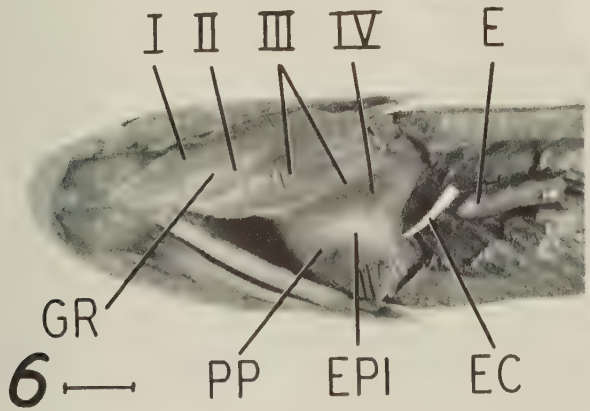
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FISH POPULATIONS IN AND AROUND BRUSH SHELTERS OF DIFFERENT SIZES PLACED AT VARYING DEPTHS AND DISTANCES APART IN DOUGLAS LAKE, MICHIGAN *

IMMANUEL A. RODEHEFFER

IN FORMER numbers of the Michigan Academy *Papers* the writer has presented various data on the use of brush shelters by fish and on the movements of marked fish in Douglas Lake, Cheboygan County, Michigan (Rodeheffer, 1939, 1940, 1941). As these studies progressed and public interest in lake improvement increased it became apparent that answers were needed to numerous problems which had already been suggested in "The Improvement of Lakes for Fishing" (Hubbs and Eschmeyer, 1938). Scientists, fisheries managers, and fishermen wanted practical answers to many urgent questions.

At what depth should artificial fish shelters be placed in a lake to be most suitable for certain species favored by anglers? Do the young, the half-grown ones, and adults of such species have individual depth preferences? Among the many factors which may govern the optimum depth for shelters consideration may be given to the species of fish for which protection or utilization is desired, the seasonal movements of the fishes, temperature (particularly during the summer months), extent of light penetration, relative amounts of deep and shallow water in a lake, ice and wave action, fluctuations in water level, and types of bottom at various depths.

Another question that puzzles the individual who attempts to improve a lake by installing shelter devices is, How many shelters should be put in a given area, or how far apart should such constructions be placed for maximum efficiency? It is self-evident that numerous factors must be considered when answering this question, such as the available food supply, the habits of the species for which

* Contribution from the Institute for Fisheries Research of the Michigan Department of Conservation and the Biological Station of the University of Michigan.

protection is desired, the amount of bottom area suitable for shelters, the funds available for the work, and the abundance of natural cover.

Shall a few large shelters or numerous small ones be installed in a lake? This is a question often asked after several shelters have been built and placed. Much brush and much labor are required to build large shelters. They are difficult to handle and place where wanted. Economy in the building and placement of large and small shelters is dependent upon the materials and the equipment immediately available. The suggestion has been made that small shelters be built for young fish and large shelters for "keeper" fish (Hubbs and Eschmeyer, 1938 : 66). Limited testing has supported the value of the proposal.

During the summer months of 1941 and 1942 studies designed to answer these questions were undertaken on Douglas Lake at the University of Michigan Biological Station.

ACKNOWLEDGMENTS

Again the writer acknowledges with gratitude the coöperation of Dr. A. S. Hazzard, director of the Institute for Fisheries Research, in planning this work and interpreting the data. Dr. A. H. Stockard, director of the Biological Station of the University of Michigan, offered advice and equipment. As in former studies, the guidance in this investigation and the help given in the preparation of this report by Dr. Carl L. Hubbs have been invaluable. The funds necessary to carry on this work were provided by the Institute for Fisheries Research of the Michigan Department of Conservation. The Fish Division of the Michigan Department of Conservation, through Mr. O. H. Clark, furnished the labor required. Professor W. F. Ramsdell, of the University of Michigan School of Forestry and Conservation, supplied means of cutting and transporting the brush used in the construction of shelters. To these individuals and others who made this undertaking possible the writer offers his sincere thanks.

FISH POPULATIONS IN AND AROUND BRUSH SHELTERS PLACED AT DIFFERENT DEPTHS

To obtain evidence on the optimum depth for the placement of brush shelters six shelters of the hollow-center type (Hubbs and Eschmeyer, 1938 : 80–81, fig. 20) were installed on the shoals of North

Fish-Tail Bay, in Douglas Lake, two each at depths of five, ten, and fifteen feet. This region was selected for two main reasons: (1) The terrigenous bottom slopes evenly to a depth of twenty feet or more, with only moderate differences in angles of slope; (2) The bottom is of sand, covered by a thin layer of flaky marl. The area thus provided a uniform habitat without vegetation or bottom irregularities, which might have concentrated the fish locally. The shelters, similarly constructed and spaced at equal intervals, could therefore be assumed to present approximately equal availability and attraction, except for the one factor being tested, that of depth of water. Furthermore, the bottom was favorable for seining, so that the total fish population in and about each structure could be caught periodically for counting.

The experiment was run in duplicate. The six shelters were placed in pairs 200 feet apart, with one pair on the 5-foot contour, one pair on the 10-foot contour, and the other two at 15 feet. The outermost structures were about 400 and 500 feet from shore. The pairs were staggered in such a fashion that no shelter was nearer than 200 feet to any other.

STRUCTURES AND EQUIPMENT

The shelters were made as nearly identical as possible. Scrub-oak and maple poles were used for the frames, which consisted of an inner unit 9 feet square, with the ends of the poles protruding beyond the square, and a surrounding frame 11½ feet square. The larger unit was fastened to the protruding ends of the smaller one in such a way as to make a sturdy base for the brush. The brush, consisting of maple, scrub oak, tag alder, and cherry, was placed in bundles about 18 inches in diameter at the butt end and laid on this frame, with the tops pointing away from the center. Each bundle was securely wired to the pole of the inner frame with number 9 galvanized wire. All bundles were placed as close together as possible, so as to form a complete circle. The outer edges were trimmed, making each shelter 18 feet in diameter. The double framework provided a flat surface on the bottom which permitted the net to slide under the shelter when it was raised to the surface. To facilitate raising, a special bridle was attached to the four corners of the inner frame, with a sufficient length of wire to allow the apex of the bridle to be fastened to a float.

A specially constructed fine-meshed bag seine was used for capturing the fish populations around these shelters. This seine, 158 feet in length, was made with a center section, of $\frac{1}{4}$-inch square mesh, which formed a bag 8 feet long, 8 feet wide, and 12 feet deep, tapering to 4 by 4 feet at the closed end. On each side of the bag for 47 feet the seine was 12 feet deep and made of $\frac{3}{8}$-inch mesh. The end sections, 28 feet in length and tapering to 6 feet in depth, were of $\frac{3}{4}$-inch mesh. The seine was equipped with sufficient floats to keep it upright in the water and with enough weights to hold the lead line on the bottom. The net was laid from a boat outside a shelter in such a fashion that the device was completely encircled. Ropes fastened to the brails led to shallow water, and thus allowed the net to be pulled shoreward under the shelter immediately after the structure was hoisted to the surface. While being hauled toward shore the seine was pursed by keeping the brails together, so as to prevent the escape of the fish already in the net and the capture of any fish in the water between the shelters and the beach. For seining the fish from the shelters in 15 feet of water a straight seine 5 by 100 feet made of $\frac{7}{8}$-inch mesh was fastened to the top of the center section of the bag seine.

In earlier experiments with brush shelters (Rodeheffer, 1939, 1940, 1941) the structures were pulled to shallow water after being enclosed by the net. When the fish had been gathered the shelter was replaced in its original position. To save time, labor, and wear on the shelters Dr. A. S. Hazzard suggested that a floating hoist be used for lifting the shelters to the surface, so that the seine could be pulled under them. The hoist that was constructed (Fig. 1) had a base 25 by 25 feet. Nine oil drums, later increased to thirteen, were fastened at the corners of this hoist to give it buoyancy. Poles extending upward from the corners of the square were brought together to form an apex twenty feet above the surface of the water. The framework was equipped with a steel cable extending from a geared drum and a hand-operated crank secured at one of the corners, passing upward through a fixed pulley at the peak and downward to the surface of the water. At this point the cable was threaded through a movable pulley, brought upward, and fastened to the fixed pulley at the top. The pulley was hooked onto the bridle attached to the shelter, after the floating hoist had been anchored over the shelter. The turning of the crank wound the

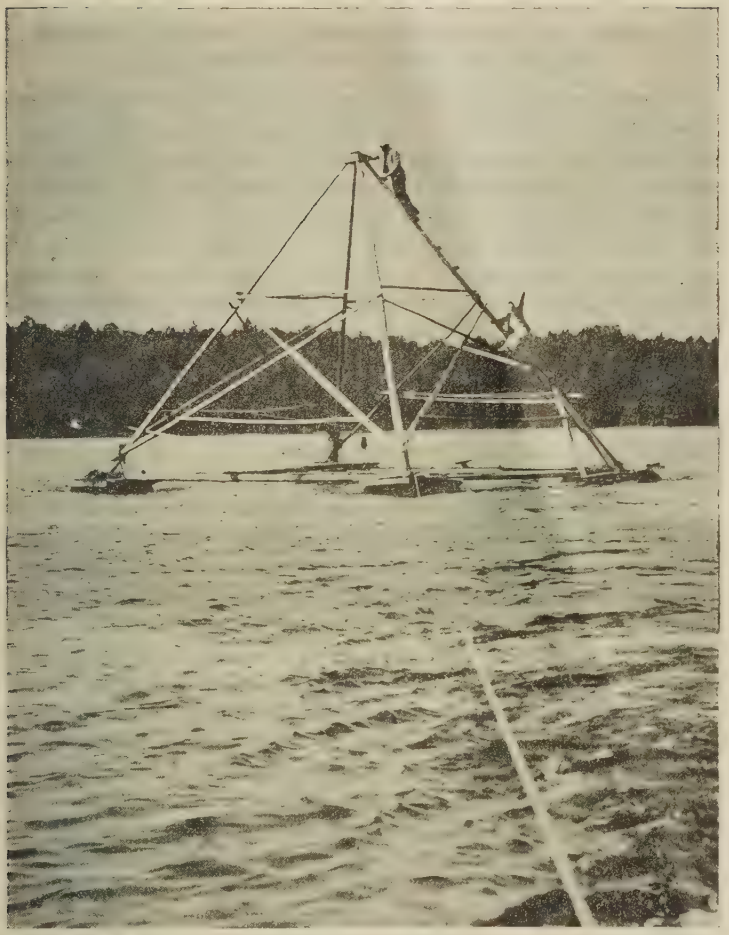

FIG. 1. Hoist used in lifting brush shelters. The device is being towed to the site of a shelter

cable on the drum, and thus lifted the installation to the surface (the power ratio of the block and tackle and gears was 1 : 34). After the seine had been hauled through the area, the shelter was lowered to its original position.

NUMBER AND SIZE OF FISH CAUGHT AT DIFFERENT DEPTHS AROUND SHELTERS AND IN CONTROL AREAS

To secure data on the fish living in and around the six shelters these shelters were lifted in daylight a total of thirty-five times at intervals of two to nine days during July and August of 1941. All captured fish were identified, measured, and counted, with the results shown in Table I. After the shelter had been replaced the fish were returned to the water over it. The open waters, treated as control areas, between and on the sides of the shelters, were seined three times at each depth. When the control areas were being seined the net was laid in a circle to cover an area similar to that encircled when taking fish in and around a shelter. While the net was brought shoreward the brails were kept together to prevent the capture of fish from waters other than the designated control areas. These seinings formed a basis for a comparison of the fish population in and around shelters and in similar places without protection.

The number of fish of some species per haul, particularly the yellow perch, increased at the greater depths. The number of perch per haul was less than 3 in the shelters placed at the 5-foot depth, increased to 142 per haul from the shelters in 10 feet of water, and mounted to almost 1,000 per haul from the shelters in 15 feet of water. It is possible that even greater numbers of young perch would be protected by shelters placed deeper than 15 feet. Control areas yielded only 4 perch per haul at the 10-foot depth, and none at 5 or 15 feet. The perch from the shelters at the three depths varied little in size. The modal-size class was 5–6 cm. at all depths. There is another common size (age group?) at about 11 cm. Only 6 perch of legal size (6 inches or more) were recorded, all from shelters in 15 feet of water. The fact that perch are markedly dwarfed in Douglas Lake (Weller, 1938) may account for the limited size range. Large schools of small fish (estimated to be 2–3 cm. long), so densely crowded as to give the water a bluish-green tinge, sometimes rose to the surface when a shelter was being lifted from 15 feet of water and, occasionally, from a shelter at the 10-foot depth. Capture of a few of these with a hand net revealed them to be young yellow perch. The shelters harbored thousands of these fish, but they were too small to be retained by the net and hence are not included in the table.

TABLE I

NUMBER PER HAUL AND SIZE (TOTAL LENGTH IN CENTIMETERS) OF FISH OF EACH SPECIES TAKEN FROM HOLLOW-CENTER BRUSH SHELTERS PLACED AT DIFFERENT DEPTHS IN DOUGLAS LAKE, MICHIGAN

Species *	Number per haul at given depths			Size range at given depths			Average size at given depths		
	5 feet (10 hauls)	10 feet (13 hauls)	15 feet (12 hauls)	5 feet	10 feet	15 feet	5 feet	10 feet	15 feet
Game fishes	...	...	0.1	...	...	63.0–63.0	...	...	63.0
Northern pike	2.7	142.2	996.5	5.0–13.4	3.1–14.7	3.5–21.7	7.7	5.5	5.4 †
Yellow perch	7.0	6.2	1.3	4.3–22.2	4.2–18.7	5.7–25.3	7.7	7.9	10.7
Smallmouth bass	29.1	15.7	3.3	3.5– 7.2	3.1– 8.2	3.5–10.5	5.3	4.9	5.9
Largemouth bass	0.3	0.2	...	10.0–15.3	9.8–14.6	...	12.2	12.2	...
Bluegill	55.2	60.0	56.3	1.9–17.1	1.5–19.0	1.9–19.7	8.3	8.3	9.0
Pumpkinseed	67.0	64.8	44.7	2.1–21.6	2.5–19.7	2.3–28.5	8.9	8.2	11.5
Rock bass									
Coarse fishes									
Sucker	0.2	0.2	0.5	37.9–40.6	37.8–41.8	5.9–39.8	39.0	38.8	22.5
Bullhead	0.3	0.5	0.8	6.2– 7.4	4.7– 7.1	4.4– 7.0	6.8	5.8	5.9
Forage fishes									
Common shiner	0.3	...	0.7	5.3– 6.0	...	5.2–11.0	5.8	...	8.3
Spottail shiner	3.5	7.2	90.8	2.7– 6.7	1.9– 9.3	1.5– 9.3	5.1	4.8	5.0 †
Sand shiner	1.2	0.2	3.2	2.1– 7.2	1.6– 6.0	4.4– 7.6	4.3	4.5	6.3
Mimic shiner	...	...	0.6	...	...	2.2– 6.0	...	...	3.6
Log perch	0.7	21.5	37.3	4.7–10.6	5.3–10.6	4.3–12.5	9.1	8.9	8.9
Johnny darter	2.5	5.7	5.0	3.1– 5.8	2.1– 6.1	3.3– 7.1	4.6	4.4	4.7
Iowa darter	0.2	0.8	0.4	3.4– 4.4	2.9– 5.7	3.6– 5.5	4.0	4.8	4.8
Muddler	...	0.1	0.1	...	2.8– 2.8	7.0– 7.0	...	2.8	7.0
Total fish per haul	170.2	325.3	1,241.6	...	...	...	...	...	...
Total fish taken	1,702	4,226	14,899	...	...	...	...	...	...

* The scientific names are listed at the end of the article.

† Only a percentage of the perch between 3 and 7 centimeters and of the spottail shiner between 4 and 6 centimeters were measured; the others were merely counted. The average sizes for these species are based on actual measurements taken.

Certain other species, such as the largemouth and the smallmouth bass, showed a definite preference for the shelters in shallower water. Shelters in 5 feet of water harbored almost twice as many largemouth bass as those in 10 feet of water and about nine times as many as those placed at 15-foot depths. The shallowest shelters produced more than five times as many smallmouth bass as the deepest ones and slightly more than the shelters in 10 feet of water. Young smallmouth bass, although present in small numbers, appeared consistently in every haul from the shelters in 5 feet of water. This substantiates former findings (Hubbs and Eschmeyer, 1938 : 64). Largemouth bass were taken in greater numbers than the smallmouth bass, but this is possibly due to the type of bottom, which is a flaky marl. The young of these species, having a size range of 3 to 10 cm., were the most common, with a scattering of smallmouth bass 14 to 25 cm. long from the shelters at all three depths. No fish of legal size (10 inches or more) were caught. Nine seinings of the control areas netted a total of only 6 young smallmouth bass at the 5-foot depth and 2 in 10 feet of water. Only one largemouth bass was taken in the 10-foot controls, and none was captured at the 5-foot depth. No largemouth or smallmouth bass were taken from the controls in 15 feet of water.

The pumpkinseed, ranking second in abundance in shelters on the 5- and 15-foot contours and third in shelters in 10 feet of water, was found in about equal numbers at all depths. Nor was there any marked difference in the minimum, maximum, average, or modal size of the fish taken from the shelters at the stated depths. Two sizes are commonly represented, one of about 3 to 4 cm. and the other of about 7 to 8 cm. Only a few (18) were of legal size (6 inches or more). That this fish seeks protection is apparent when one considers that no pumpkinseeds were taken from the shallow controls, only 2 from the control areas in 10 feet of water, and just 1 from the controls at the 15-foot depth.

The number of rock bass taken from the shelters showed a slight but gradual decline with increasing depth of water. Hauls from the shelters on the 5-foot contour averaged about 1.5 times as many rock bass as those on the 15-foot contour. Rock bass 7 to 8 cm. long were particularly common around shelters at all three depths, and constituted almost one third of all the rock bass taken. However, enough larger rock bass were taken from the deep shelters to increase

the average size from 8 to 9 cm. for the shelters in 5 and 10 feet of water and to 11.5 cm. from the shelters at the 15-foot depth. This increase was primarily due to the number of fish taken in the size range between 8 and 15 cm. Only 32 of the 316 fish 8 cm. or more in length were of legal size (6 inches or more). The percentages of legal-sized fish among the rock bass caught from the shelters on the 5-, 10-, and 15-foot contours were 3.7, 1.2, and 6.0, respectively. Although fewer rock bass inhabited the shelters in the deepest water, those found there included the highest percentage of legal size. No rock bass were taken in the seinings in the control areas.

The almost total absence of northern pike in the shelters was surprising, for Douglas Lake is known as a good pike lake. These fish are commonly caught in the larger weed beds, which in places extend from shallow water to a depth of about 18 feet. The capture of only one northern pike from a shelter in 15 feet of water indicates that this fish does not seek such a habitat.

Very few bluegills were taken about the shelters, but this does not indicate a lack of preference for brush cover on the part of this species. Bluegills are not common in Douglas Lake. Artificial plantings have been made, but these fish do not seem to reproduce naturally to any extent. Seining of waters where one might expect to take bluegills seldom yielded any results.

Several of the forage fishes were well represented in the catches from the shelters. The spottail shiner sought protection in the deeper shelters. Ninety-one fish per haul were taken from the deepest water, whereas only 7 fish per haul were seined from the 10-foot contour shelters and fewer than 4 per haul were caught in shelters on the 5-foot contour. Only one spottail was taken from the control areas, and it was at the 10-foot depth. Only a little variation in size was noted from all three depths. Most of the fish were young and half grown.

The largest numbers of log perch were found in the deeper water adjoining the shelters. The average catch was less than one fish per haul from the shelters in 5 feet of water. This increased to over 21 fish per haul from shelters on the 10-foot contour and to more than 37 fish per haul from the shelters in 15 feet of water. Seining of the control areas at the 10-foot depth netted almost 6 fish per haul. No fish were taken at the two other depths. The average size was about 9 cm. at all depths.

The Johnny darter, well known as a fish of the open bottom, was captured in comparatively small numbers in the shelters — about 5 fish per haul from shelters on the 10- and 15-foot contours, and 2.5 per haul from the shelters at the 5-foot depth. In the control areas this species averaged more fish per haul than any other. Seining of the controls at the 10- and 15-foot depths captured 5 fish per haul and from the 5-foot control areas the hauls netted an average of 15 fish.

Almost all suckers caught were adults. In the control areas the 3 suckers captured at 15 feet and the 6 taken at 10 feet were full grown. The one fish taken at 5 feet was young, being 7 cm. long.

Other species seined in the shelters listed in Table I were recorded in such small numbers in both the control areas and the shelters that conclusions are not warranted.

The total catch of fish per seine haul from the shelters increased with an increase in depth. Brush shelters placed on the 5-, 10-, and 15-foot contours averaged 170, 325, and 1,241 fish per haul, respectively. It should be noted, however, that these figures are largely influenced by the perch catch.

Control areas at the same depths averaged 13, 16, and 8 fish per haul. These numbers emphasize the fact that fishes in general seek shelter.

FISH TAKEN FROM SHELTERS PLACED 50 AND 200 FEET APART

The determination of the most desirable concentration of shelters in a lake was one of the major projects for the summer of 1942. To provide information on this subject fish collections were made from brush shelters placed 50 and 200 feet apart. For this experiment eight hollow-center shelters were used. Four of these were placed on the 8-foot contour, 50 feet apart. The other four were located at the same depth but at a distance of 200 feet from one another. To reduce the cost and to save labor the six constructions made in 1941 to test the effectiveness of such devices at different depths were used. Two additional shelters were built in 1942 in replica of the six already made. All these were placed in North Fish-Tail Bay in the same locality where they had been used the summer before. Fish populations were determined as in the previous experiment, by means of the hoist and the large seine. The determinations were made only for the two center shelters in each

group. To reduce the variables the two newly built shelters were placed at the ends. Fish of all species taken from the installations and from the control areas between the shelters were identified, counted, and measured (Table II). A study of the data reveals little variation in the average size of the fish netted from either group of protection devices.

The capture of northern pike in shelters 50 feet apart arouses interest. The data presented are too scanty to warrant definite conclusions, but they suggest that this species may utilize close-set shelters.

Yellow perch averaged about 114 fish per haul from the brush constructions separated by 200 feet, and 51 per haul from those set 50 feet apart. None of the 1,022 fish taken in the shelters that were 200 feet apart were of legal size, and only 5 of the 559 fish caught in the more closely placed covers were 6 inches or more in length (it should be noted again that the perch of Douglas Lake are greatly stunted). Control areas of 200 and 50 feet between shelters yielded an average of 2.2 and 3.8 fish per haul, respectively.

Rock bass also concentrated more heavily in brush constructions separated by the greater distance. Shelters 200 feet apart produced 367, or an average of 41 per haul. Eight of these were 6 inches or more in length. Only 234, or 21 per haul, were netted from shelters 50 feet apart. Nine of these were legal-sized fish. No rock bass were taken in hauls from the control areas.

Smallmouth bass, brown bullheads, and log perch, although taken in small numbers, showed a similar tendency to collect in larger numbers in shelters separated by the greater distance. Smallmouth bass averaged 2.1 and 0.4 fish per haul from shelters separated by 200 and 50 feet. Only 3 fish from the more widely separated shelters were of legal size. Control hauls caught 0.3 fish per haul between the devices placed close together and 0.2 per haul between those farther apart. The brown bullhead averaged 2.4 fish per haul from shelters set 200 feet apart and 0.9 per haul from those separated by a distance of 50 feet. None were taken in the control areas. The log perch produced 3.6 and 1.6 fish per haul from the shelters separated by distances of 200 and 50 feet, respectively. The larger control yielded 4 fish per haul; the smaller one, 3.

The largemouth bass were netted in approximately equal numbers (about 6 per haul) from each group of shelters. Almost all the

TABLE II

Number per Haul and Size (Total Length in Centimeters) of Fish Taken from Hollow-Center Brush Shelters Placed Different Distances Apart in Douglas Lake, Michigan

Species	Number per haul at given distances		Size range at given distances		Average size at given distances	
	200 feet (9 hauls)	50 feet (11 hauls)	200 feet	50 feet	200 feet	50 feet
Game fishes						
Northern pike	0.2	1.4	26.8–47.5	17.3–192.0	37.0	35.6
Yellow perch	113.6	50.8	4.8–14.5	5.5– 20.3	9.8	9.9
Smallmouth bass	2.1	0.4	2.8–40.5	13.5– 16.0	16.2	14.8
Largemouth bass	5.8	5.9	3.3–35.0	3.2– 35.3	5.9	5.8
Bluegill	0.3	0.6	7.0– 7.7	7.2– 8.6	7.5	8.4
Pumpkinseed	69.7	75.6	2.3–18.6	2.2– 17.3	6.4	5.3
Rock bass	40.8	21.3	2.1–19.8	2.7– 18.5	9.4	9.2
Coarse fishes						
Sucker	0.8	0.2	33.0–42.7	37.3– 39.0	38.8	38.5
Bullhead	2.4	0.9	10.2–15.5	6.5– 15.7	13.3	12.1
Forage fishes						
Spottail shiner	0.4	1.4	4.2– 4.5	2.1– 4.8	4.5	4.0
Sand shiner	...	0.4	...	2.8– 3.7	...	3.5
Log perch	3.6	1.6	6.7–10.7	8.5– 10.4	9.6	9.5
Johnny darter	0.9	2.4	3.7– 5.5	3.3– 5.8	4.6	4.4
Iowa darter	0.3	0.5	4.0– 5.5	4.2– 5.6	4.8	5.2
Muddler	...	0.1	...	3.0– 3.0	...	3.0
Total fish per haul	240.9	163.5	...	...	...	...
Total fish taken	2,168	1,797	...	...	...	...

fish were young, only one legal-sized fish being taken from shelters in each group. Control areas between the devices separated by a distance of 50 feet averaged 2 young largemouth bass per haul. None were caught in the others. Adams and Hankinson (1928 : 481) observed that the largemouth bass showed a decided preference for areas with an abundance of vegetation and also that the young over an inch in length were solitary. Placing shelters close together may make not only the shelters but the areas between them a good habitat for the young of this species.

The pumpkinseed congregated in slightly larger numbers in shelters set close together. The average haul netted about 76 pumpkinseed from installations placed 50 feet apart and 70 fish from those located 200 feet apart. Open waters between the artificial covers installed 50 feet apart yielded 7.5 fish per haul, or more than twice the number (3.6 per haul) taken between shelters sunk 200 feet apart. Almost all fish taken in the shelters and the controls were young, with a modal size of 3 to 4 cm. Probably other age groups at 6 to 7 cm. and 9 to 10 cm. are represented in the pumpkinseed populations. Only one legal-sized fish was netted from the shelters placed close together. Nine legal-sized fish were taken from the other shelters.

The spottail shiner and the Johnny darter, although poorly represented in the hauls, averaged more in shelters placed close together. The few suckers taken in the shelters and the one taken in the wider open water were all adults. Other species, namely, the bluegill, the sand shiner, the Iowa darter, and the northern muddler, were caught in such limited numbers in both the shelters and controls that interpretations are not attempted.

Shelters placed 200 feet apart yielded 240 fish of all species per seine haul. Those 50 feet apart averaged 163 fish per haul. The shelters spaced four times as far apart yielded 1.5 times as many fish per shelter. More fish per unit length of shoreline were therefore sheltered when the constructions were placed closer together, though fewer fish were then concentrated about each installation. The open water between shelters, designated as control areas, harbored more fish when shelters were placed close together. These control areas, which were seined nine times, produced 18 fish per haul between the shelters 50 feet apart and 13 fish per haul between those placed at the greater distance.

FISH TAKEN IN AND AROUND BRUSH SHELTERS OF DIFFERENT SIZES

In order to determine the relative effectiveness of shelters of different sizes six structures of the ladder-shaped type (Hubbs and Eschmeyer, 1938 : 74–79) were built and installed in 1942. Three of these were trimmed to $16 \times 12 \times 3$ feet, and three were made $8 \times 6 \times 3$ feet. The smaller ones, therefore, had one half the area and one fourth the volume of the larger. Except for size all were as nearly identical as possible. The available brush (cherry, ironwood, beech, oak, and maple) was closely packed, and the shelters were installed on the 8-foot contour along the south shore of Bryants Bay. Here the clean and fairly hard packed bottom is largely composed of sand, clay, and some rocks ranging in size from that of a baseball to that of a man's head. The area is devoid of aquatic vegetation. Conditions along the line of installation were rather uniform. The shelters, alternately large and small, were spaced 200 feet apart.

Again the hoist and net employed in former operations were used to catch populations in and around the shelters. Fourteen hauls were made from the larger shelters and 17 from the smaller ones. The fish from all six shelters were identified, counted, and measured (Table III). Areas between shelters were seined five times to furnish a comparison of fish populations in and around shelters as contrasted with those in the open areas in this part of Douglas Lake.

Rock bass were taken in the ratio of 5 to 12 from the small and the large shelters. More legal-sized fish were netted from the bigger constructions, where 44 fish 6 inches or more in length were captured. Twenty-nine legal fish were caught from the other shelters. However, the greater percentage of these fish came from the smaller shelters, which harbored 8.4 per cent, whereas the larger ones yielded only 6.5 per cent.

Pumpkinseed were also found in greater numbers in the larger shelters. Here they averaged 29 per haul. In the smaller shelters the average haul netted about 19 fish. Two dominant size classes are represented, 5–6 and 9–10 cm. in total length; the smaller ones were somewhat more abundant in the smaller shelters; the larger ones were more common in the larger shelters. Only 4, or about 1.0

TABLE III

NUMBER PER HAUL AND SIZE (TOTAL LENGTH IN CENTIMETERS) OF FISH TAKEN FROM LARGE AND SMALL LADDER-SHAPED BRUSH SHELTERS IN DOUGLAS LAKE, MICHIGAN

Species	Number per haul from different shelters		Size range from different shelters		Average size from different shelters	
	16 feet (14 hauls)	8 feet (17 hauls)	16 feet	8 feet	16 feet	8 feet
Game fishes						
Northern pike	0.1	...	16.2–16.7	...	16.5	...
Yellow perch	24.4	27.2	7.5–16.0	6.0–15.5	10.6	9.8
Smallmouth bass	1.9	1.2	5.1–38.2	5.2–39.0	23.0	16.9
Largemouth bass	1.2	1.3	3.4– 6.1	3.5– 5.7	4.4	4.5
Bluegill	0.4	...	7.2– 8.3	...	7.8	...
Pumpkinseed	28.9	18.6	2.6–20.6	2.0–20.1	8.5	8.5
Rock bass	48.1	20.3	2.4–26.6	2.7–27.8	11.1	11.1
Coarse fishes						
Sucker	1.5	0.6	35.9–41.0	34.6–40.7	38.8	38.8
Bullhead	0.2	0.1	3.3– 5.9	3.2– 3.2	4.5	3.2
Forage fishes						
Common shiner	...	0.1	...	4.7– 4.7	...	4.7
Spottail shiner	5.2	14.8	2.0– 5.0	2.0– 4.0	3.0	3.0*
Sand shiner	1.0	3.8	5.0– 7.0	5.2– 8.3	6.0	6.4
Log perch	2.3	1.6	5.5–10.5	9.2–10.0	9.5	9.9
Johnny darter	0.3	0.2	3.3– 4.5	2.5– 4.5	3.8	3.5
Muddler	0.1	...	2.7– 7.0	...	5.0	...
Total fish per haul	115.6	89.8	...	...	...	...
Total fish taken	1,618	1,527	...	...	...	...

* Only a small percentage of the spottail shiners were measured. The others were merely counted. The average size given for this species is based on actual measurements.

per cent, of the 404 pumpkinseed from the 16-foot constructions were of legal size, whereas 7, or 2.2 per cent, of the 317 fish from the 8-foot installations were of legal size.

The yellow perch was the most common fish from the 8-foot shelters, where an average of 27 per haul was netted. The bigger shelters produced 24 per haul. The larger number of perch recorded for the small shelters is primarily due to one haul of 171, and most of this particular school of fish were 8 to 9 cm. in length. Another size group of 11 to 12 cm. was also found in the smaller shelters. Only one legal fish was taken from the shelters of each size.

Largemouth bass and smallmouth bass averaged between 1 and 2 fish per haul from either size of shelter. All largemouth bass netted were young fish between 3 and 7 centimeters in length. Of the 26 smallmouth bass caught around the 16-foot shelters, 10, or 38.5 per cent, were legal-sized. From the 8-foot shelters, 6, or 30 per cent, of the 20 fish netted were over 10 inches in length.

The spottail shiner was the most abundant of the forage fishes. Almost 3 fish per haul were taken from the small shelters for every one caught in the larger ones. This difference in populations around these brush constructions is mostly due to one haul from the middle 8-foot, shelter, from which 125, or about one half of the total number of spottail shiners from the small shelters, were netted. The white suckers, although netted in small numbers, were all adults. The sand shiner, caught in limited numbers, was more common in the smaller shelters. The few log perch seemed to show a preference for the larger shelters.

Except for the smallmouth bass a comparison of the average sizes of all species from the small and the large shelters shows little difference.

Five hauls made through the areas between the shelters netted two 16-cm. pumpkinseed, or 0.4 fish per haul, and 74 log perch, or 18.5 fish per haul. The perch averaged 9.3 cm. in length. Two smallmouth bass, 13 and 45 cm. in total length, and one Johnny darter of 3.5 cm. were found in the control seining.

CONCLUSIONS AND SUGGESTIONS FOR FISH MANAGEMENT

The conclusions stated here are based on five summers' experiments in providing shelter for fishes in Douglas Lake, Michigan, supplemented by limited earlier work in other lakes by Dr. R. W.

Eschmeyer (Rodeheffer, 1939 : 188). No attempt has yet been made to determine whether such devices will increase the total productivity of fishes in a lake. Rather, the aim has been to ascertain so far as possible the practicability of such constructions and the extent of their use by the various species of fish living in a lake. The value of these conclusions is impaired because we do not know the relative abundance of the various species in Douglas Lake. It may be stated, however, that rock bass, yellow perch, pumpkinseed, smallmouth bass, largemouth bass, and northern pike are present in sufficient numbers (although unquestionably in varying degrees of abundance) to tempt fishermen to angle for these species. Bluegills are not common. In general, fish shelters located in barren parts of a lake attract primarily the young and half-grown fish of certain species (Rodeheffer, 1939). There is a change, however, in such populations by night and by day (Rodeheffer, 1940). If fish are transported from the part of a lake where brush constructions are located, others will repopulate such areas (Rodeheffer, 1940).

More work needs to be done on the effectiveness of fertilizers in the increase of vegetation in and about shelters before definite conclusions regarding this suggested practice can be justified.

Shelters placed in deep water harbor more fish, particularly yellow perch, spottail shiners, and log perch, than those located in shallow water during the warm summer months, although the reverse is true for largemouth and smallmouth bass and rock bass. When shelters are located varying distances apart, those separated by the greater distances support larger populations of yellow perch and rock bass, whereas pumpkinseed are somewhat more abundant in and around shelters placed close together. Likewise, a comparison of the fish populations in and around large and small installations reveals greater concentrations of fish in the larger shelters. This is notably true of rock bass and pumpkinseed. Yellow perch occur in somewhat smaller numbers in the large shelters.

These studies on the effectiveness and utilization of brush shelters suggest certain conclusions regarding fish management. It is clear that given types of lake improvement will affect the several kinds of game fish in different ways. With full realization that this work covers only one phase of the complex problems involved in the management of lake fishes, the writer now discusses and suggests some of the possible applications, under headings giving the

names of the species that are most commonly taken about the shelters.

Rock Bass

Young and half-grown rock bass were the most common fish consistently caught in and around the brush constructions placed on the 5- to 6-foot contour in Douglas Lake. However, when the fish from a shelter were transported to another part of a lake the number of rock bass in subsequent seinings was always less than that in the first seining. In like manner, the number in night hauls was always smaller than in those by day, and their average size was less (Rodeheffer, 1940). These fish also show the greatest tendency to live at or to return to the same refuge (Rodeheffer, 1941). Shelters placed at a greater depth or located closer together attract fewer rock bass. Small shelters harbor fewer rock bass than large ones.

It should not be difficult to increase the number of rock bass in a lake if this should be desired. Adams and Hankinson (1928 : 499) found them generally distributed in Oneida Lake and in shallow water, an indication of a preference for areas with abundant aquatic vegetation and stony bottom. Their partiality for cover is well known to anglers and ichthyologists. It has been shown that this species seeks artificial cover in Douglas Lake. It is likely that the number of this fish may be increased in a given body of water by placing adequate brush shelters in the lake, granted, of course, that other conditions, such as spawning facilities, are adequate. If, on the other hand, rock bass are found to be overabundant and stunted, as they are in some northern Michigan lakes, it may be desirable and possible to control their number by destroying their spawning beds, or by giving preferential treatment to other species, by placing artificial shelters in deeper water, and by building small shelters. Or it may be practicable, particularly if other species which are to be encouraged use the same habitat, to build and place these shelters where they will attract the rock bass in great numbers, so that the excess may be taken out for other use by the method of seining employed in the experiments here reported.

Yellow Perch

Yellow perch were common around all shelters, but the increased concentration around those in deeper water shows that they have

a decided preference, at least during the summer months, for constructions so placed. These fish were found to be more numerous at night, both in shelters and on the open shoals in shallow water, than during the day. If yellow perch were removed from a shelter and transported to another part of a lake, others would move in until the original population was approximately duplicated. Marking of these fish shows that they seem to live in or come back to the locality where first taken during a season. Few were seined there the following summer. Shelters located far apart harbored more yellow perch than those placed close together. It is questionable whether the size of a brush construction is a factor controlling the number of yellow perch that use it as a habitat. If an increase of the yellow perch is desired, such constructions should very likely be placed in deep water. Shelters may be used by perch for spawning or, if it is considered advisable, a brush carpet may be installed for this purpose (Hubbs and Eschmeyer, 1938 : 83). When these fish are abundant and stunted, as they are in Douglas Lake, control may be aided by limiting the number or by locating shelters in shallow water. If northern pike occur in the lake, placing shelters close together at the depths of weed beds inhabited by pike may attract these predaceous fish into the area, where they may help to keep the perch under control. Seining of the fish around shelters in fairly deep water and destroying those of which there is an overabundance may be helpful. The use of a localized poison, such as rotenone, in killing fish in shelters might also be practicable, provided the shelters do not harbor desirable species that should not be destroyed.

Northern Pike

Northern pike, although abundant in Douglas Lake, were seldom found around brush constructions in either shallow or deep water when they were separated by several hundred feet. Shelters placed close together (50 feet apart) harbored enough pike to permit one to conjecture that, if the encouragement of pike is desired, they should be placed fairly close together and arranged so as to cover a considerable area. It has been observed that the best catches of northern pike by fishermen are generally made close to large weed beds, which, in a barren lake, might be simulated by a concentration of shelters.

Pumpkinseed

The pumpkinseed is another game fish that is abundant in Douglas Lake. It shows a decided preference for brush installations, although an unequal concentration is represented around shelters placed in different parts of the lake. In Douglas Lake, North Fish-Tail Bay, with its somewhat quiet water and marl bottom, harbored more young and half-grown fish around the shelters than did other parts of the lake where brush constructions were located. The depth of a shelter seemed to make little difference to fish of this species, but they did prefer those shelters placed closer together. Large constructions make a hiding place for more fish of this species than small installations. As with other species, large numbers desert the covers at night. If they are taken from a shelter and transplanted to another part of a lake, the original concentration will be approached by others coming in.

Provided spawning and other conditions are satisfactory, the pumpkinseed may be encouraged by supplying an abundance of cover, natural (weed beds) or artificial (brush constructions). If possible, a part of a lake, such as a bay resembling a pond with comparatively quiet water, should be chosen.

Control of number should be possible by limiting the shelter available, placing artificial covers in parts of a lake not conducive to pumpkinseed or by destroying the spawning beds.

Largemouth and Smallmouth Bass

Not many largemouth and smallmouth bass were taken around shelters in the various parts of Douglas Lake. At Grapevine Point on the lee side of prevailing winds, where the shoals are clean and sandy, the smallmouth bass predominated. In North Fish-Tail Bay, which is partly sheltered, with a bottom composed of sand covered with flaky marl, the largemouth bass were more common. In Bryants Bay, which is more exposed than either of the other two places mentioned, and where the bottom is composed of packed sand, clay, and rocks, largemouth and smallmouth bass were not numerous, but a larger percentage of the smallmouth bass were legal-sized fish. When both species were captured from the shelters and transported to another part of the lake it was found that other fish sought the shelters in numbers about equal to those transplanted. Both large-

mouth and smallmouth bass were seined from shelters and control areas by night and by day, but there were fewer in either place at night than during the day. Largemouth bass, although taken in smaller numbers, revealed a greater preference for the shelters. A larger percentage of marked smallmouth bass were recaptured around the shelters, which indicates a somewhat limited population in such areas.

Neither species displays any particular preference for large or small shelters. Their solitary nature, rather than the size of shelter, may be the controlling element. Smallmouth bass indicate some preference for shelters far apart. Largemouth bass inhabit in about equal number shelters either far apart or close together, but more of them seem to occupy the areas between shelters when they are placed close together. The young of both species were collected in larger numbers in brush installations placed in 5 feet of water than in those placed at a depth of 10 or 15 feet. Environments should be chosen that are well adapted to the species desired. Shelters should be placed in shallow water, and numerous small ones will probably prove more effective than a few large ones, at least for the largemouth bass.

If it should be desirable to control the number of these fish, it is suggested that the amount of shelter be limited or that such constructions be placed in deeper water. The amount of spawning can, of course, also be controlled.

Forage Fishes

Several species of forage fish were taken about shelters in sufficient number to warrant conclusions regarding their use of such structures and to permit suggestions that may be of value in fisheries management. The aim of the experimental work was to test the practicability of improving conditions for game fishes rather than for forage species. It may be possible to construct special devices or to place them so that they will be particularly enticing to individual species of forage fish.

With few exceptions the spottail shiner was taken in small numbers. This probably was due to the fact that most of the constructions were placed in fairly shallow water, on the 5- to 6-foot and 8-foot contours. This fish was found in much larger numbers around shelters placed in 15 feet of water than about those in shallow

water. Small shelters at a depth of 8 feet harbored almost three times as many of these fish as larger shelters similarly placed. From the limited evidence presented it is suggested that small shelters be put in deep water (about 15 feet) and fairly close together (50 feet or less apart), if the aim should be to increase the production of this forage fish.

In Douglas Lake the log perch was found inhabiting shelters placed in 15 feet of water many times more abundantly than those in shallow water. It is questionable what rôle it plays in the welfare of most of our game fishes.

Other species were represented in the shelters. Very few were taken, either because there were not many in the lake or because they preferred some habitat other than that where the shelters were installed.

FURTHER INVESTIGATIONS REQUIRED

As experimental work with brush shelters progresses, many additional problems are presented. What kind of shelter is the most efficient, the circular, ladder, hollow-square, single-log, tree, clump, brush carpet, deadhead, stump, stone, tile, or others that may be devised? Are some more desirable for certain species, or for the young or the half grown or the adults of such species? What kinds of brush shall be used in constructing them? Does the water which becomes tea-colored around those made of scrub oak and evergreens become objectionable or even toxic to fish? Should shelters be placed in certain areas fairly close together to resemble large weed beds or should they be spaced at regular intervals along the shores of a lake? Are those anchored on a sharp drop-off more effective than the ones on the shoal? Are artificial constructions superior or inferior to similar natural protection areas (weed beds)? Will they aid in starting aquatic vegetation and, if so, what kinds of shelters are most satisfactory and where, in what part of a lake, and on what kind of bottom should they be placed? Will shelters increase the food supply of fishes and, if they do, what kinds are most satisfactory for this purpose? What effect will the placing of fertilizer in the shelters have on such food production? How long will they last when properly submerged? Thus we may go on with questions that a practical fisheries manager asks when he attempts to improve a lake with such devices.

At present large hollow-center brush shelters lying in parts of Douglas Lake which are under observation are exposed to the prevailing winds. Some of these are supplied with black soil to see whether aquatic vegetation will grow in them. Two unsuccessful attempts have been made to plant aquatic vegetation, and it is hoped that continued observations and, possibly, additional plantings may be made. Spring planting is suggested, for the unsuccessful attempts were made in July and August.

A study of the food growing on or being harbored by shelters seems of vital importance. Such an investigation might show the food available for all sizes of desired species from fry to adults. It may be feasible to develop shelters that will be particularly conducive to the increase of the forage fish populations. In experimental work so far conducted little has been done to introduce improvements for the forage fishes.

Studies of individual lakes with little cover are in progress at present. It is hoped that, when populations are known, such lakes may be improved with artificial shelters to what may be considered ideal conditions. Population studies should then be continued to determine the effect of the shelters on the production of fish.

Many brush shelters and spawning beds have been installed in Michigan lakes since the beginning of 1933. Plans are being made for a careful check of some of these installations to determine their durability and the extent to which they have aided in the establishment of aquatic vegetation and to learn to what degree they are being utilized by fish. Far too little checking of fish management practices has been undertaken.

SUMMARY

Experiments in Douglas Lake with brush shelters placed at 5-, 10-, and 15-foot depths indicate that:

1. Shelters at a depth of 15 feet harbor about seven times as many fish as those on the 5-foot contour. The ones at 10 feet offer cover for about twice as many fish as those at the 5-foot depth.
2. Yellow perch are by far the most common fish in the shelters lying in the deeper water.
3. Pumpkinseed inhabit in about equal number shelters submerged at the stated depths.

4. Rock bass show a slight but gradual increase in number as the depth of the shelter is decreased.

5. Young largemouth and smallmouth bass show a preference for shelters in 5 feet of water.

The trials with shelters spaced 50 and 200 feet apart reveal that:

1. Shelters put 200 feet apart protect about 1.5 times as many fish per unit as those 50 feet apart.

2. Yellow perch and rock bass are about twice as abundant in the shelters farther apart.

3. Smallmouth bass are more common in the shelters separated by 200 feet.

4. Largemouth bass are found in about equal number in either group of shelters, but given areas between the closely set shelters produce more largemouth bass than similar areas between the shelters farther apart.

5. Pumpkinseed gather in somewhat greater number in shelters 50 feet apart.

6. Northern pike congregate in larger number in shelters close together.

Data gathered in the work with small and large shelters support the views that:

1. Large shelters harbor more fish than small ones.

2. Rock bass and pumpkinseed are found in greater number around the larger shelters.

3. Yellow perch are more common around the smaller shelters.

4. Largemouth and smallmouth bass are found in approximately equal number around the shelters of each size.

These findings support the conclusions that, if artificial covers are to be effectively used by certain desired species of fish, their placement must vary accordingly. Rock bass prefer large shelters spaced far apart and submerged in comparatively shallow water of about 5 or 6 feet. Pumpkinseed seek large shelters on the quiet, protected shoals, set at any convenient depth but preferably close together. Largemouth and smallmouth bass collect in the large or small shelters in shallow water of about the 5-foot depth. Yellow perch find most desirable small shelters sunk in water about 15 feet

deep, and northern pike seem to seek those which are placed close together.

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APPENDIX

List of Scientific and Common Names of Fishes Mentioned in this Report

Common white sucker	*Catostomus c. commersonnii* (Le Sueur)
Northern common shiner	*Notropis cornutus frontalis* (Agassiz)
Great Lakes spottail shiner	*Notropis hudsonius hudsonius* (Clinton)
Northeastern sand shiner	*Notropis deliciosus stramineus* (Cope)
Northern brown bullhead	*Ameiurus nebulosus nebulosus* (Le Sueur)
Northern pike	*Esox lucius* (Linnaeus)
Yellow perch	*Perca flavescens* (Mitchill)
Northern log perch	*Percina caprodes semifasciata* (De Kay)
Central Johnny darter	*Boleosoma nigrum nigrum* (Rafinesque)
Iowa darter	*Poecilichthys exilis* (Girard)
Northern smallmouth bass	*Micropterus dolomieu dolomieu* Lacépède
Largemouth bass	*Huro salmoides* (Lacépède)
Common bluegill	*Lepomis macrochirus macrochirus* Rafinesque
Pumpkinseed	*Lepomis gibbosus* (Linnaeus)
Northern rock bass	*Ambloplites rupestris rupestris* (Rafinesque)
Northern muddler	*Cottus bairdii bairdii* Girard

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TESTICULAR ASYMMETRY IN THE WOODPECKER *COLAPTES* *

FREDERICK H. TEST

EARLY in the course of field work to gather material for a study of coloration in the woodpecker genus *Colaptes*, commonly called flickers, I noticed that the left testis differed strikingly in shape from the right. Records were kept of this asymmetry in subsequent collecting, and these form the basis of the present report. Most of the data were collected on field trips sponsored by the Museum of Vertebrate Zoology of the University of California. I am grateful to the director, Dr. Alden H. Miller, for permission to publish these records.

The testes of birds lie opposite to each other, dorsal to the anterior part of the peritoneal cavity and on the ventral side of the elongate, irregularly shaped kidneys. In form the testes vary somewhat from species to species, but most commonly they are approximately oval or ellipsoidal. Van den Broek (1933, p. 96) has indicated the shapes of avian testes as oval (as in the fowl *Gallus*, and other birds), round (as in the sparrow, *Fringilla*), elongate (as in the grebe, *Colymbus*), almond-shaped (as in the bustard, *Otis*), attenuate (as in *Halicus*, a genus I have been unable to identify), and vermiform (as in the swift, *Cypselus*). In most species left and right testes have approximately the same shape. A slight difference has been recorded in pigeons by Riddle (1918), the left being longer and more slender than the right, which usually has a slightly greater bulk. Chapin (1939), in discussing an African woodpecker of the genus *Campthera*, says ". . . the left testis, which is apt to be slightly larger, often exhibits a very unusual shape, being bent abruptly outward at the anterior end." He found this condition in several specimens of four species (two races of one) belonging to this genus, and he notes that he has seen a similar condition elsewhere only in *Colaptes auratus*.

Most of my records refer to the Red-shafted Flicker (*Colaptes*

* Contribution from the Department of Zoology, University of Michigan.

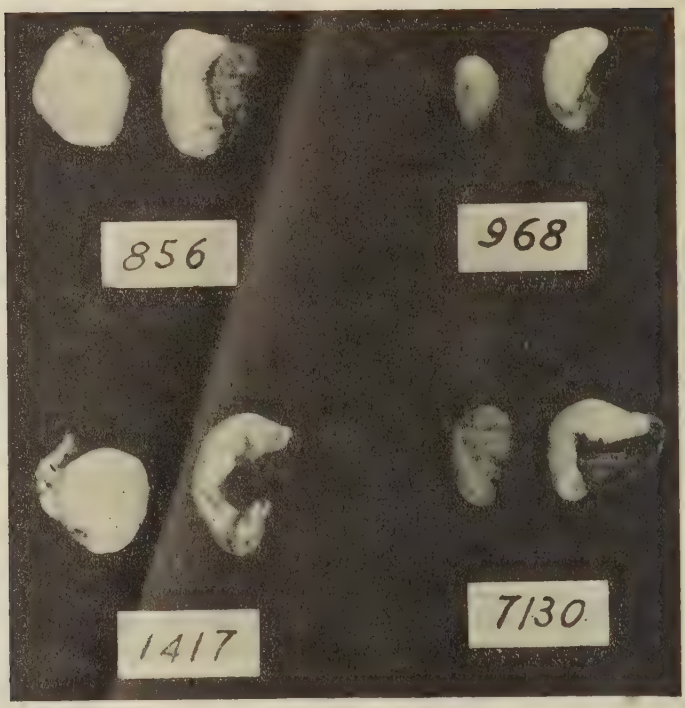

FIG. 1. Pairs of testes from four breeding individuals of *Colaptes cafer*, showing some of the typical variation in form. × 1⅔

cafer). In this species the right testis in the adult (Fig. 1) is approximately oval or elliptical in outline. The left testis usually has a smaller short dimension and is about half again as long, tapering to a blunt point anteriorly. The anterior half or less of the left testis extends laterad, forming a considerable angle with the posterior part, which lies approximately parallel to the long axis of the body. Occasionally there is a constriction at the bend. Table I shows that in thirty-one left testes from breeding birds for which I have adequate data the bend is a 90-degree angle in most of the birds. Two specimens have only a small laterally projecting process on the anterior end. One (Fig. 2, No. 985) shows no angulation, being elliptical in outline, a little longer and more slender than its mate.

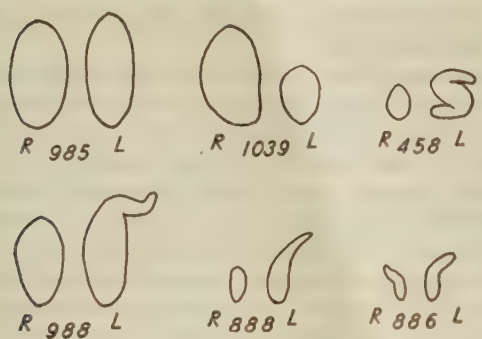

FIG. 2. Outlines of pairs of testes from six specimens of *Colaptes*. *C. cafer:* adults, nos. 985, 458, 988; juveniles, nos. 888 and 886. *C. auratus:* adult, no. 1039. × 2

Another gonad (Fig. 2, No. 458) is unique in that it forms a sharply bent S. In two of the gonads with a 90-degree bend the anterior tip is bent forward at a large angle to the laterally projecting segment (Fig. 2, No. 988).

TABLE I

ANGULATION OF THE LEFT TESTIS IN *COLAPTES*

Birds	No angulation	< 45°	45°	50–85°	90°	Total records
C. cafer						
Breeding adults	1	1	2	2	25	31
Nonbreeding adults	0	4	7	0	5	16
Juveniles	0	0	3	0	0	3
C. auratus						
Breeding adults	1	0	3	0	3	7
Nonbreeding adults	0	0	1	0	1	2
Juveniles	0	1	2	0	0	3
C. chrysoides, adult	0	0	1	0	0	1

Table I also shows that sixteen left testes from adult nonbreeding flickers average somewhat different in form, the largest number having an angulation of about 45 degrees. This suggests that the annual growth of the testes preparatory to breeding commonly

causes the left one to become more sharply angled than it is in the quiescent condition of winter.

I have few records for juvenile Red-shafted Flickers. Each of the three available has an angulation of about 45 degrees (Fig. 2, No. 888), showing that the asymmetry of the testes is present at least as early as the fourth week after hatching. Two of these juveniles have the right testis, as well as the left, turned outward at the anterior end, but only the tip is turned, and the whole gonad is decidedly shorter than the left one (Fig. 2, No. 886).

In bulk the left testis is usually somewhat smaller than the right. The volumes of four typical pairs of testes of breeding birds, determined by displacement of liquid, are shown in Table II.

TABLE II

VOLUMETRIC COMPARISONS IN CUBIC CENTIMETER OF RIGHT AND LEFT TESTES OF *COLAPTES CAFER*

	No. 928	No. 967	No. 945	No. 1417
Right testis	0.40	0.20	0.27	0.35
Left testis	0.30	0.20	0.22	0.40

The fewer records available for the eastern yellow-shafted flicker (*Colaptes auratus*) present a picture similar to that just described. In seven breeding adults (Table I) the left testis had an angulation of about 45 degrees in three and of 90 degrees in three. A single bird (Fig. 2, No. 1039) had an oval left gonad, like that of the right side but considerably smaller. Of the two records for nonbreeding adults one shows a left testis with a 45-degree angle; the other, a 90-degree bend. The three available records for juveniles are of an angulation of 45 degrees or less.

A single record for a nonbreeding Gilded Flicker (*Colaptes chrysoides*) exhibits a left testis bent outward at a 45-degree angle.

DISCUSSION

It is pertinent to ask whether the asymmetry described above is inherent in the gonads and their *Anlagen* or whether it is a result of environmental factors. Material is not at hand for a study of the morphogenesis of flicker testes, but a few suggestions and obser-

vations may be recorded here. The left testis was longer than the right in all but one of the specimens examined, which would suggest that this asymmetry is inherent, although its primary cause is not indicated. The bending laterad of the anterior end of the left gonad, however, is occasionally absent and is commonly variable in degree. This indicates that the environment of the developing testis may be, in part, responsible for its final shape.

In the chick the genital ridges differentiate just posterior to the origin of the vitelline arteries and near the mid-line of the body, in fact, immediately laterad to the dorsal mesentery. It is probable that these ridges form in a similar location in *Colaptes*. A logical explanation for the bent testis thus seems to be that the germinal epithelium differentiates so far forward on the left side as to include some of the tissue on the posterior side of the base of the vitelline artery. The growing gonad would then of necessity come to assume the same curve or angle as that between the vitelline artery and the posterior part of the dorsal aorta. That the right testis usually is not curved probably is due to a shorter genital ridge which does not extend as far forward as the vitelline artery. In this connection it seems important to note that the posterior ends of the two members of each pair of testes in the juvenile and adult flickers I have examined were at approximately the same anteroposterior level. Being longer, the left gonad thus had its anterior end well ahead of that of the right, and there is no apparent reason for believing that one has migrated in relation to the other in the course of development.

It is evident from Table I that, as pointed out before, the left testis assumes a more sharply angled form as it enlarges preparatory to the breeding season. The explanation for this change may be completely environmental, a result of the growing testis pushing against some relatively unyielding organ anterior to it and being forced to assume a right-angled bend. The testes are situated near the anterior end of the peritoneal cavity, and the organs there are considerably crowded and unyielding. Unfortunately, no data are at hand to prove or to disprove this hypothesis. Another possible explanation suggests itself. There may be a difference between the inner and the outer curvatures of the left testis such that the greater curvature undergoes a greater increase in length in the enlarging testis than the lesser curvature does. Such a difference might be

in the tension of the tunica albuginea or of the covering peritoneum. The result would be a change in curvature as the gonad enlarges.

As Friedmann (1927) has suggested, it seems probable that normal testicular asymmetry has no relation to a disturbed sex ratio. Riddle, in 1918, published observations on pigeons which correlated a sex ratio in favor of the male, with a testicular asymmetry in offspring resulting from interspecific and intergeneric crosses and also in some diseased individuals. In these birds the left testis was larger than the right oftener than in healthy birds from intraspecific matings. This, however, is a very different thing from the usual and normal occurrence of asymmetry in wild populations.

A distinct asymmetry such as that described above may prove to be of value in establishing additional evidence of phylogenetic relationships. This is dependent, of course, on the cause of the asymmetry, whatever that cause may be, being inherited. So far as is now known, this type of asymmetry is confined to the woodpeckers (Picidae). It occurs in genera other than *Colaptes* and *Campthera*, but too few data are available to enable me to judge its incidence accurately. Field sketches are at hand for male gonads of one Red-breasted Sapsucker (*Sphyrapicus varius*), three Downy Woodpeckers (*Dryobates pubescens*), two Hairy Woodpeckers (*Dryobates villosus*), and two California Woodpeckers (*Balanosphyra formicivora*). In one individual of each of the last two species the left testis was longer and curved slightly laterad in the anterior part. All others were symmetrical.

Here is a problem on which field collectors could gather a large amount of information incidental to their main objectives and with little loss of time. It is routine with many collectors to measure one testis as an indication of breeding condition. Because of the asymmetry in some species, a record of whether the left or the right testis is measured should always be kept. Little additional time would be consumed if an outline, to scale, of both testes were sketched in the field catalog.

The author is grateful to Dr. A. E. Woodhead for assistance in making the photographs here reproduced.

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THE VALUE OF MUSSEL DISTRIBUTION IN TRACING STREAM CONFLUENCE

HENRY VAN DER SCHALIE

INTRODUCTION

THE application of the distribution of mussels in streams to geomorphic problems has been a controversial subject for the past fifty years. The disagreement rests mainly on the interpretation of established facts dealing with the life history, ecology, and distribution of these animals. So far as I can judge from the historical development of this controversy, there are mainly two groups: (1) a few geomorphologists and workers in other fields who follow Johnson (1905) in the contention that stream confluence is but one of several ways by which fresh-water mussels have managed to go from one drainage basin to another; and (2) several malacologists, including some of our best students of the naiades, such as the late Dr. A. E. Ortmann and Dr. Bryant Walker, who have attempted to show that confluence is essentially the best explanation for the natural distribution patterns found at present.

Considerable difficulty has resulted in the course of the controversy because of confusion in regard to the specific group of shells to which we are limiting ourselves. In order to keep the issue clear and to arrive at any sensible evaluation of the relative merits of the evidence presented, it is important at all times that we realize that we are concerned only with fresh-water mussels and not with the gastropods or the Sphaeriidae that may be found with them. It is generally known that small isolated bodies of water will often in some unknown manner become populated with snails and fingernail clams. Just how this populating takes place is as yet largely a matter of speculation, and considerations of these questions, along with the

EDITOR'S NOTE — In 1943 this paper won first place in a competition for the Walker prizes in natural history sponsored by the Boston Society of Natural History. Contests are held annually. It was the intention of the founder of the fund, the late William Johnson Walker, to encourage the younger research workers in their investigations. E. S. McC.

evaluation of naiades as indicators of stream confluence, invariably lead to confusion and muddle our thinking. At the outset, then, it is necessary to stress the condition that we have to do with but one group of animals, the mussels, which are highly specialized biologically and tend to behave in a very characteristic manner in matters pertaining to their life history, ecology, and distribution. These facts have been well established, and it is largely because we have some sound and basic biological concepts within this group of animals that we can use the evidence presented to good advantage in tracing former stream connections.

HISTORY OF THE CONTROVERSY

The controversy began shortly before the turn of the century. Hayes and Campbell (1894), in a discussion of the geomorphology of the southern Appalachians, called attention to some geological and physiographical indications to support their theory that the Tennessee River formerly flowed southward to the east of the present Walden Ridge and, following a path across a low divide into the present Alabama River system, emptied into the Gulf of Mexico. They suggested that a tributary of the Sequatchie River cut through Walden Ridge near the close of the Tertiary period and tapped the headwaters of the Tennessee, causing it to flow due west, as we now find it.

Biologists soon lent support to this theory. Simpson (1900) gave credence to the hypothesis on the strength of the distribution of mussels common to both the Alabama and the Tennessee rivers. A year later Adams (1901) offered additional faunal evidence which he believed essentially indicated that a former connection existed between these two major drainage systems. He stressed the supposition, however, that sufficient time had elapsed to permit specific differentiation between the animals of these rivers.

In 1904 Johnson spent two weeks in the Chattanooga district to evaluate the physiographic and geologic evidence for such a confluence. In a thesis published a year later (1905) he said:

> In summing up the evidence which has been presented in favor of the theory of a recent westward diversion of the Tennessee from a former southward course, it has been pointed out that while the facts noted in that connection admit of a rational interpretation on the basis of capture, they are to be explained just as readily and satisfactorily entirely independent of that theory.

It is possible that this statement constitutes a sound physiographical interpretation. Nevertheless, the faunal evidence implies that there had been a confluence between the Tennessee and the Alabama rivers. Johnson (1905) attempted to show that Simpson's faunal evidence was not satisfactory by pointing out that the distribution of certain species he used to prove such a confluence was contradictory. Actually, so far as the argument is concerned, Johnson appears to have the better of the situation. Fortunately, in science only *facts* are acceptable. As a pioneer Simpson was all too ready to speculate on distribution patterns that were not well established. More thorough students would certainly not subscribe to some of his statements, much less to certain of his speculations which claim that birds are important passive agents in the extension of the distribution of naiades.

In 1913 Ortmann published his paper on the influence of the Alleghenian Divide upon the fresh-water fauna. The introduction to this work referred to the "Tennessee–Coosa" problem. Although he devoted only a footnote to the controversy considered here, he summarized his stand in this issue so well that it deserves a complete statement:

> This is the problem in which Johnson (1905) is especially interested. The old idea is (see chiefly Hayes, 1899) that the headwaters of the Tennessee once continued in the direction of the Coosa (*Appalachian River*), and that the present course of the Tennessee is due to a deflection in consequence of stream capture. Johnson believes (and also White, 1904) that the present course of the Tennessee is original, and I consider his physiographical evidence as perfectly sound and satisfactory. But since the Najades (and other freshwater groups) have been used to demonstrate the correctness of the assumption of the existence of the Appalachian River (see Simpson, 1900b, p. 133, Adams, 1901, p. 846, and Ortmann, 1905, p. 130), we must take cognizance of this line of evidence, and dispose of it in some way. Johnson did this by dismissing it as not convincing, as not apt to demonstrate stream capture. However, as I have said, he is wrong in this, and I believe the distribution of the Najades *does indicate stream capture in this region*, but in the opposite direction: the original fauna belonged to the old Tennessee (similar to the present in its course), and certain southern tributaries of it have been captured by the Coosa–Alabama system. This idea is already implied in Simpson's (1900b, p. 135) sentence: "It is probable that nearly all the Unionidae of the Alabama River system have been derived from the Tennessee," and White (1904, p. 38) directly says that the upper course of the original Walden Gorge River (tributary to Tennessee) has been captured by Conasauga River (tributary to Oostanaula and Coosa Rivers.)

We must emphasize that Ortmann did not question Johnson's evaluation of the physiographical evidence, but he was nevertheless

convinced that the distribution patterns of the mussels in this critical region show that *stream confluence* has taken place. The exact place and method may be open to question, but there is factual evidence to indicate that the Tennessee and the Alabama rivers were once connected.

Unfortunately, Ortmann and Johnson did not pursue this issue further. The matter rested till 1938, when van der Schalie (1938b) published the results of a study of the mussels of the Cahaba River in northern Alabama. This work again suggested that there were formerly connections between these major drainage basins. The general conclusions drawn from the facts presented were as follows:

> It seems necessary to conclude that in geologically recent time tributaries of the headwaters of the Alabama drainage were connected with tributaries of the Tennessee drainage. This confluence permitted the three creek species known to belong to the Tennessee drainage to enter the headwaters of the Alabama drainage.
>
> The seven representative species which entered the Alabama River system from the north by way of the Tennessee drainage indicate that streams somewhat larger than creeks were connected. Since these forms are at present more or less differentiated in the two river systems, sufficient time must have elapsed to permit differentiating evolutionary tendencies. Thus, the connection of the larger streams must have preceded that of the creeks.

These pronouncements brought an immediate response from Johnson (1939), who suggested that they avoided the main issue, which, according to him, is: "Do these mussels require fresh-water connections between two streams in order to pass from one to the other?" An answer to this question was given by van der Schalie (1939a) in an article which stressed the following important considerations:

1. In spite of the series of published records by naturalists on observations of fresh-water mussels attached to the feet of aquatic birds, "no one has ever established that fresh-water mussels *have actually been transported from one stream to another in this manner.*" When this matter was brought to the attention of Dr. H. A. Pilsbry at a meeting some time later, he suggested that we failed to note an important point in this connection, that is, that the birds seen with mussels attached to their feet were crippled or dead birds, and he did not feel that such birds were important distribution agents.

2. Another strong piece of evidence against the distribution of mussels by birds is the fact that most species have "a characteristic

distribution pattern within one or more of the major drainage systems. Such patterns would not be likely to develop if mussels were haphazardly carried about from stream to stream by birds."

3. Life-history studies indicate that naiades are a unique group. "Protagonists of passive migration of mussels by means of aquatic birds fail to take into account the life-history requirements of our Naiades. All North American fresh-water mussels are parasitic in their larval stage on some species of fish before they are capable of beginning life in the environment in which we find them."

4. Many species of mussels are highly specific in their ecological demands. "Assuming that a mussel which accidentally attached itself to the foot of an aquatic bird were a gravid female, and that that mussel with its potential glochidia (also an assumption because glochidia are shed at specific periods) reached a body of water belonging to another drainage, it would yet not necessarily establish a colony of mussels there, because the particular fish host which carries that particular species of mussel would necessarily have to become parasitized to complete the life cycle of the mussel. Also, even if one assumes that all this did happen by chance, the ecological demands for most species of mussels are such that the young mussel dropping from a fish would have to arrive in an environment suited to it, a condition which adds materially to the hazards involved."

5. Finally, there is an abundance of evidence to show that the very regions where malacologists find a "mingling" of mussel species are also the areas in which geologists and physiographers have given facts to prove the existence of zones of confluence. Attention was called to the presence of such areas in:

(*a*) Michigan, Ontario, and New York, where postglacial waters connected the Mississippi and the St. Lawrence rivers;

(*b*) The region of the upper Red River of the North, where a confluence permitted certain Mississippi naiades to enter the waters flowing north to Hudson Bay;

(*c*) The zone mentioned by Simpson (1893) as "the southern end of the mountain range," which presumably refers to the supposed connection between the Tennessee and the Alabama rivers;

(*d*) Finally, the region of Yellowstone Park, where a confluence appears to have occurred between the headwaters of the Missouri and the Snake rivers over a divide known as Two-Ocean Pass.

The confluences just mentioned are merely the ones most generally recognized among malacologists and geologists as important and clearly defined connections with an attendant influx of species. Others will be mentioned later in this paper.

The preceding contentions by van der Schalie were considered in some detail by Johnson (1941, 1942). Unfortunately, his involved hypothetical discussions failed to take into account published information giving several definite distribution patterns. These patterns cannot be explained at present unless we recognize that well-authenticated biological facts force us to rely on the evidence that mussels are carried across divides by fishes during a period of confluence. Reference will be made later to these unfortunate omissions of factual information. As a result of a mere suggestion that confluence is not the only method by which mussels manage to cross drainage divides, we should not, then, assume that the basic work of able malacologists such as Simpson, Ortmann, and Walker is of no significance in the solution of problems involving former drainage. Johnson's statements, nevertheless, imply as much. In the light of what is known it seems unwarranted and foolish not to give the zoogeography of naiades at least fair consideration.

It is possible that additional geological information will soon be available to aid in the solution of the Tennessee–Alabama drainage problem. A communication from Edwin C. Eckel, chief geologist for the Tennessee Valley Authority, contains the following statement:

"We have in preparation right now a very large report — probably some four to five hundred pages — on the regional geology of the dams. To that I am prefixing a summary of the more important features of the region, and in that summary I am giving some space to consideration of the geologic history of the river itself."

Since we are forced by the involved nature of this drainage problem to await further evidence for its solution, may I suggest that we turn to the Michigan area, where the present drainage systems have been established in comparatively recent time? The main events in the postglacial development of the rivers in this state have been well determined by careful studies of a number of competent geologists. Certainly there is no conflict among them and geomorphologists regarding postglacial drainage in Michigan like that found in a region as complex historically as the Gorge in

Walden Ridge. In fact, it seems sound for us to consider postglacial drainage changes here and their relations to mussel distribution in the nature of a laboratory test to determine whether basic correlations actually exist between confluence and the distribution patterns of the naiades. If there are strong indications that confluence is the usual and most effective means to establish the distribution patterns of mussels, it would seem essential to guard against giving unwarranted weight to other hypothetical means of dispersal among this specialized group of animals. Furthermore, if we are to accept a precept fundamental in geology, that we interpret the past in terms of the present, it is imperative that we give due consideration to the logical method for the dissemination of these animals, particularly when in nature a series of well-established events are correlated so convincingly.

DISTRIBUTION OF NAIADES IN MICHIGAN

Southeastern Michigan

It was in southeastern Michigan that students of naiades first noticed the importance of confluence in relation to mussel distribution. It is a striking fact that practically all the sixty species in this area are a Mississippi River assemblage and not, as one might normally expect in a consideration of present drainage conditions, members of the group of species common to the lower St. Lawrence River. Walker (1913) expressed the opinion, now widely accepted, that the "pre-glacial fauna of the St. Lawrence system was absolutely exterminated during the glacial period." He also stated that the Mississippi fauna now found in Lake Erie consists of "postglacial immigrants from the south and [is] not the result of any survival in that region of any part of the pre-glacial fauna." According to him, the present fauna in Lake Erie is due to an invasion from the Mississippi Valley through the Maumee River outlet into postglacial Lake Maumee.

Ortmann (1924) elaborated upon this invasion and showed that a particular stage in the postglacial lake development is of great significance in accounting for contemporary naiad distribution in the present tributaries of Lake Erie. He proved that three distinctive river species of mussels in those tributary streams in northern Ohio are not found in Lake Erie itself, and yet these same three species occur in the Maumee River. This condition is generally known as

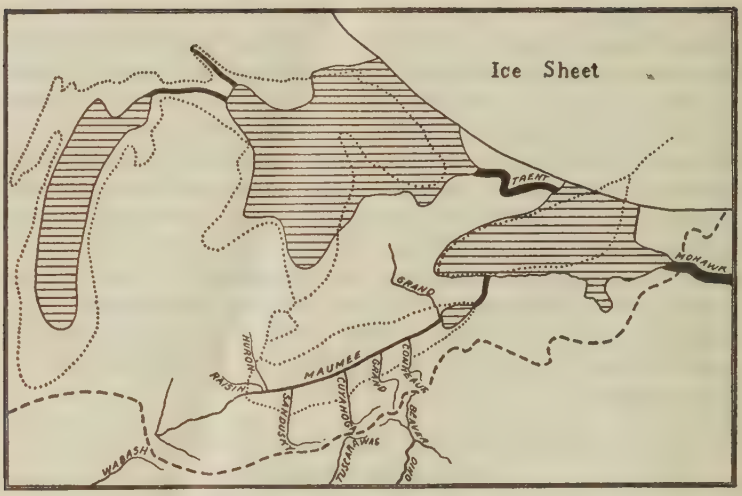

FIG. 1. Trent outlet stage of the Great Lakes

discontinuous distribution. By recourse to postglacial history of the region Ortmann was able to show (see Fig. 1) that during the Trent–Nipissing stage the water of the later Algonquin and early Nipissing Lake periods did *not* flow into the Lake Erie basin and that this region was almost free of impounded water, with perhaps only a remnant of the lake at the eastern end of the basin near Buffalo. These conditions permitted the Maumee River to continue through the partially dry bed of Lake Erie, and thus make the present tributaries to Lake Erie tributary to the Maumee River itself. In this way a *continuous* river pattern was established. When, at the end of the Trent outlet stage, the rising continent caused the reappearance of Lake Erie, the present *discontinuous* pattern was set for the three river-inhabiting mussels (*Alasmidonta marginata*, *Actinonaias carinata*, and *Lampsilis fasciola*).

Later, van der Schalie (1938a) showed that these same three species occur in the Clinton, Huron, and Raisin rivers of southeastern Michigan, and thus confirmed the prediction already made by Ortmann (1924), who suggested that the Huron and Raisin rivers were also a part of that Greater Maumee River system. In addition, van der Schalie (1938a) called attention to the fact that

none of these three "river" species is found in the River Rouge. Consequently, it was postulated that that drainage is "of more recent origin and has been formed since the return of the waters to the Lake Erie basin at the end of the Nipissing–Trent Lake stage in a change which caused the formation of the modern Great Lakes." Since Rouge River is confined largely to a low plain of lacustrine sand, it is not unreasonable to assume that it is topographically younger than the Clinton, Huron, and Raisin rivers. It is probable that the Rouge was never connected with the Greater Maumee, but it must be emphasized that the evidence thus far is based entirely on the distribution of the mussels it contains.

These brief statements on naiad distribution of the southeastern region of Michigan as it was brought about by confluences that occurred during the postglacial period demonstrate how closely the facts relating to the biology of this group of animals are connected with the glacial and geomorphic history of this area. There may be some who would prefer to explain these facts of distribution by any agent at all other than certain species of fish that normally carried particular species of mussels during periods (perhaps many years) when confluence existed. If we assume that birds were instrumental in effecting naiad distribution, it seems unlikely that such a striking correlation of events would exist, especially since there is reason to believe that the distribution of mussels by birds is haphazard and fortuitous. Explanation of mussel distribution on the basis of any passive agent other than the natural one (fishes) becomes even more unreasonable when we note that the ecological demands of certain species of mussels are such as to exclude them from a lake environment.

Southwestern Michigan

Van der Schalie (1941) recently published the results of zoogeographical studies conducted in southwestern Michigan. Considerable factual information was contained in tables used to show the distribution of the mussels in both the Grand and the Muskegon rivers (Fig. 2). Reference was made to the generally accepted belief that the Mississippi fauna arrived in that portion of the state at the time of confluence between the streams of that region and the Mississippi drainage by way of the Des Plaines River and the Chicago outlet to the Mississippi River. Not only does the distri-

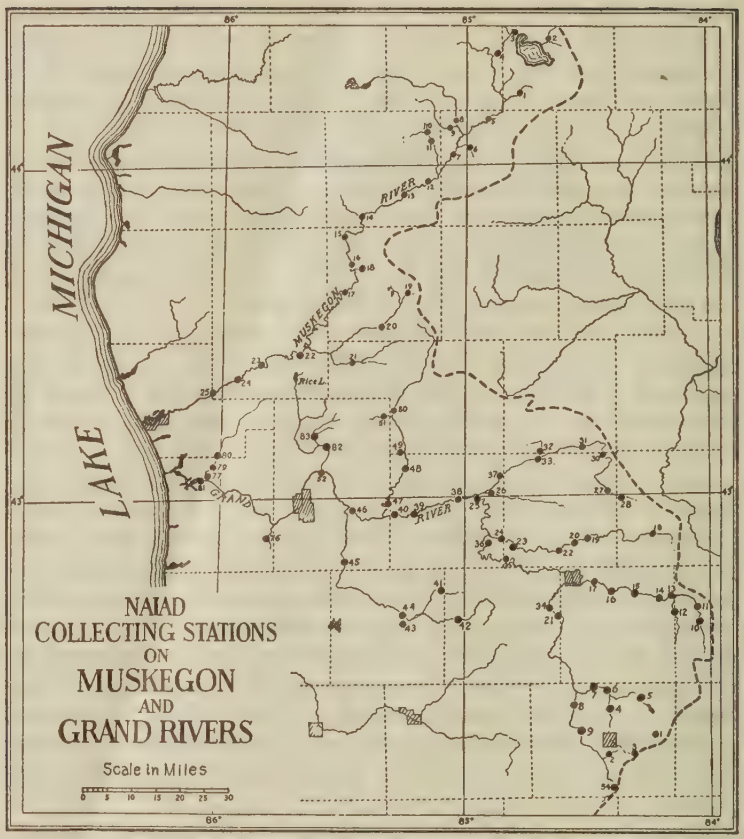

FIG. 2

bution of the fauna as a whole suggest that this assumption provides the most plausible explanation, but detailed information on the relation of the mussels in the Muskegon River to those in the Grand River indicates "that at one time in its drainage history the Muskegon River was a tributary of the Grand River. This view is substantiated by the glacial history of these streams, since it is known that the Muskegon River was at one time connected with the Grand River through the valley of the present Rouge (Rogue) River."

In the same paper van der Schalie stated that he was fully aware that "considerable skepticism exists among zoologists, geologists, and physiographers regarding the value of distributional studies of naiades in tracing stream confluence." In order to show how difficult it is to explain certain distribution patterns in any other way he cited the following examples:

> A common mussel of southwestern Michigan is *Actinonaias ellipsiformis*. It was found at many stations in the Grand River . . . . On the other hand, *Lampsilis fasciola* is well represented in the three main rivers of southeastern Michigan . . . . Both species inhabit rivers, are associated ecologically with streams of medium size, and usually are not found in the Great Lakes. Hence both are at present *discontinuous* in their respective ranges. The distribution

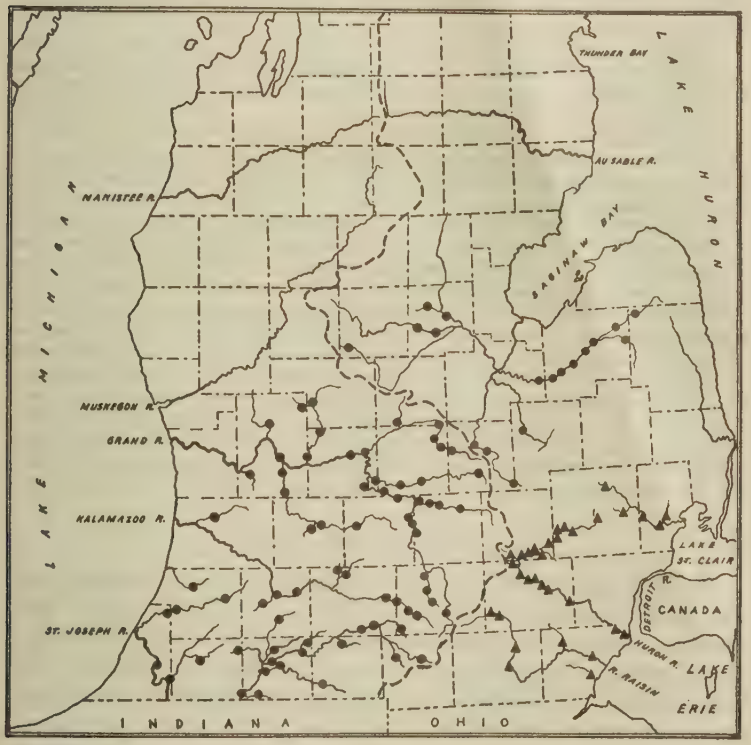

FIG. 3. Distribution of *Actinonaias ellipsiformis* (circles) and *Lampsilis fasciola* (triangles) in southern Michigan

pattern of each is shown graphically in Figure 1 [Figure 3 in this paper]. If naiades are distributed by birds and mammals, it would be interesting to have an explanation of the reason why neither of these species, *ellipsiformis* and *fasciola*, has been carried across the east–west drainage divide, particularly since the tributary streams of the two major drainage systems so closely approximate each other. Dr. Wilbert B. Hinsdale (1931, p. 6), in discussing famous portages in Michigan, points out that only a low divide separates the Raisin River from both the Kalamazoo and the Grand rivers. In regard to the divide between the Huron and the Grand rivers he says: "Mr. N. F. Wing, of Grass Lake, states that forty years ago he actually paddled across the divide between Portage River and Otter Creek, through the lowlands and swamps, without having to get out of his canoe. During high water the Indians certainly could have done the same thing; the only obstructions from Lake Erie to Lake Michigan would have been rapids and fallen timber." Nevertheless, owing to restrictions attending the ecology and distribution of naiades these species have not crossed this divide since glacial time. Certainly if birds and mammals are a factor in mussel distribution, such a restriction would not be likely to persist.

When the distribution of the species mentioned above is considered in relation to the late glacial history of the drainages inhabited by them, a remarkable set of correlations is evident. The rôle of glacial history in the distribution of *Lampsilis fasciola* has already been discussed . . . . Consequently, only the conditions affecting the distribution of *Actinonaias ellipsiformis* will be considered at this time. It not only occurs in all the rivers on the west side of the state south of and including the Grand, but has also entered the tributaries of the Saginaw drainage basin . . . . This pattern of distribution is to be expected in view of present knowledge concerning the confluence that formerly existed between the Saginaw and Grand River drainages. According to Russell and Leverett . . ., that connection persisted while Lake Warren discharged its waters across the Saginaw–Grand divide. This confluence accounts for the invasion of the Saginaw River drainage by *ellipsiformis* and other river-inhabiting species of mussels. No explanation has yet been advanced, however, for the absence of *ellipsiformis* in the Muskegon River drainage. Both *Actinonaias carinata* and *Alasmidonta marginata* probably entered the Muskegon during the period when the Grand and Muskegon rivers were connected, as has already been discussed. The fact that *ellipsiformis* did not enter the Muskegon simultaneously may mean that it invaded the Grand River drainage at a period when the connection between that river and the Muskegon no longer existed, but before the severance of the confluence between the Saginaw and Grand River drainages.

Northwestern Michigan

In 1939 van der Schalie (1939b) reported investigations carried out in the Menominee–Dickinson region adjoining Green Bay. The distribution of certain mussels of the area shows that Mississippi River naiades invaded the St. Lawrence drainage basin in this portion of the Upper Peninsula. The matter was treated in sufficient detail to bring out for the area a basic correlation between established facts in mussel distribution and the connection that formerly existed between the Fox River and the Wisconsin River at Portage, Wis-

consin. Once again detailed information concerning the ecology and distribution of the mussels implies former drainage patterns which geologists have not yet fully uncovered. That the early drainage in Green Bay and the upper portion of Lake Michigan was different from the present one is suggested in the following statement:

> In order to account for the presence of such river-inhabiting species as *Actinonaias carinata* and *Alasmidonta marginata* in the Menominee drainage basin, there must have been a continuity of *river* conditions throughout the Fox River Valley. Major difficulties in the way of this would have been the presence of lakelike regions such as Green Bay and Lake Winnebago. Leverett suggested that if we allow some seventy-five feet for tilting in the Green Bay region, there is a likelihood that the southern end of Green Bay and perhaps the bed of Lake Winnebago, which has a maximum depth of but twenty-one feet . . ., may have been nonexistent, and an ancient Fox River might have flowed in a northeastern direction through this bed.

These facts also have recently been supported by some geologists and physiographers, as was indicated by the following series of statements:

> The details connected with the matter of bringing the Menominee drainage in conjunction with the Wisconsin River by way of the Fox River Valley are not simple. According to Martin . . ., there were two rivers in the present Fox River Valley. The one, which was active during the glacial period, is still represented by that portion of the present Fox River drainage extending from Lake Winnebago to the headwaters of the Fox River at Portage [Fig. 4]. This region has the unusually small gradient of only one-half foot per mile. Such a gradient in the headwaters of a stream becomes significant when we consider that it is less than the gradient in the Mississippi River itself. In contrast to the flat grade of the upper Fox, the lower Fox River, extending from Lake Winnebago to Green Bay, drops on an average of five feet per mile. This represents a later development than that in the headwaters, and it may have some connection with the drop in lake level which Stanley (1938: 972–74) has described as occurring during a low stage in the Lake Algonquin level. The waters of Lake Michigan and Green Bay are reported to have subsided as much as 150 feet. In another paper . . . Stanley claims that the lake level may have dropped as low as 200 feet below its present level in the Green Bay area.[1] At present the depth in Green Bay opposite the mouth of the Menominee River is 114 feet. Consequently, there is no question but that the low-water stages during the Algonquin period were sufficient to give a dendritic river pattern which would have connected the lower Menominee with the greater Fox River flowing through the valley of Green Bay. In this connection, it is of interest to note that on the basis of soundings in Green Bay there is evidence that remnants of a former river valley exist in the bed of this bay. A number of other streams, including the Peshtigo and Oconto rivers in Wisconsin and the Ford, Escanaba, Whitefish, and Sturgeon rivers in Michigan, might have also been connected to form this greater Fox River system.

[1] Dr. Stanley has not yet published this paper, but he has orally confirmed the information.

FIG. 4. The Fox River drainage basin

THE PROBLEM OF DISREGARDED FACTS

The brief consideration of these three major zones of confluence in the preceding survey of areas in Michigan by no means represents

an exhaustive study of the problems involved. It is clear, however, that a sizable quantity of factual information is available on the biology of fresh-water mussels and that this information can serve as evidence in evaluating the significance of the naiad distribution for tracing stream confluence. Johnson (1941, 1942) apparently avoided taking into account the *facts* which will remain altogether unexplained unless we assume that mussels are carried across divides in the natural manner, that is, as larval parasites on fish. Numerous quotations were used in the preceding section largely to emphasize that there are, contrary to Johnson's specific charge, publications giving well-established patterns of distribution. He stated in 1942:

> It is unfortunate that van der Schalie gives only two short sentences to what he considers "perhaps the strongest evidence against the distribution of mussels by birds." We have only his statement that "most species of mussels have a definite and characteristic distribution pattern within one or more of the major drainage systems," and an expression of his personal opinion that "such patterns would not be likely to develop if mussels were haphazardly carried about from stream to stream by birds." Since these contentions go to the very root of the question at issue, it would seem that any discussion of the problem should include an adequate summary of the facts of field evidence, a clear explanation of their supposed significance, and a comprehensive statement of the reasoning based on them and the conclusions reached.

It is unnecessary to consider Johnson's (1941, 1942) long analytical discussion of the theoretical implications involved in the use of mussels as indicators of drainage change because his discussion assumed that we lack facts from which to draw conclusions. Certainly there is no objection to a difference of opinion concerning the conclusions derived from substantial factual information. It seems reasonable to expect, however, that if one disagrees with the deductions made from a careful consideration of the evidence presented other explanations which take into account the same basic facts are in order. Unless more plausible deductions are offered by those who assume that the same patterns in distribution came about by abnormal and fortuitous means, the condemnation of the original explanation (distribution by fish during periods of confluence) would appear to be without validity. At any rate, a remarkable agreement must be recognized between the information given by glacial geologists and the evidence submitted by malacologists in outlining some of the major events that are generally accepted as explaining present-day drainage systems and geomorphology.

It is clear that benefits are to be derived from the use of facts established by studies of naiades to supplement those in the closely related fields of geology and geomorphology. It is obvious, further, that a large amount of such information in these related fields awaits correlation. I submit that the difficulties encountered are not so much a matter of our inability to accumulate the essential data as of our inability to obtain the proper assistance from those best able to promote such coöperative studies.

It is my firm conviction that methods of investigation similar to those employed for the study of the correlations that exist between mussel distribution in Michigan and the postglacial history as expounded by competent geologists can also be applied to good advantage in more complex regions, such as are found in the southern Appalachians. In view of the complexity of the problems in these areas for geologists and geomorphologists it would seem reasonable that any additional clues which might aid in unraveling the tangle would be welcome. Recognition of the important rôle of zoogeography as an aid in geological and physiographical interpretation is coming more and more to the fore. Outstanding zoologists and geologists recognize this fact. A prominent zoologist (Barbour, 1926) stated: "It is in studying these changes in land form that the zoologist may by analyzing the fauna, aid the geologist and check his conclusions." Schuchert (1935), in his outstanding book on the *Historical Geology of the Antillean–Caribbean Region*, devoted a section to biogeography and showed that a clear-cut agreement is to be found between the fundamental conclusions derived from a consideration of geological history and those established by biogeographical studies of that region.

In accumulating basic facts about our North American freshwater mussels we are faced with certain practical problems which are not generally appreciated. The information gathered to date is relatively large, thanks to the careful and painstaking work of Rafinesque, Lea, Conrad, H. H. Smith, Simpson, Ortmann, Walker, and others. Much remains to be done, however, particularly in the form of critical river surveys that will give needed data bearing on the ecology and distribution of these animals. Another very serious gap in our essential knowledge is concerned with the life history and distributional relationships between specific groups of mussels and their normal fish hosts. Such studies are hampered by

a lack of interested students able to carry on a research program in a field with so little applied value, as well as by the vast changes which have come about in many of our rivers as a result of silting, the construction of power dams, and pollution from sewage and other sources. Under these circumstances the failure of outstanding geomorphologists to appreciate carefully determined truths does not serve to forward an already difficult cause. The refusal to recognize the facts of distribution available in the literature has prejudiced some individuals not only against the acceptance of the sound work of such good authorities as A. E. Ortmann and B. Walker, but also against the use of mussels as an aid in geomorphic studies. This situation is most unfortunate, for the cause of science suffers when we are not willing to correlate evidence contributed by closely related fields.

In conclusion, a statement made recently by Dr. Maurice C. Hall (1938) seems quite appropriate:

> When metaphysics abandoned the authoritarian method it developed into modern science, and when modern science anywhere accepts the authoritarian method it again becomes metaphysics. Unless we can accept the universality of natural law, the working of proportionate cause and effect, and the possibility and necessity of scientists anywhere checking the work of other scientists under different environments in order to rule out personal, local and incidental factors, we might as well abandon science and take up theology or some other subject in which the dicta of authority are accepted as *ex cathedra* statements of fact.

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SOME HORMONE EFFECTS ON THE VAGINAL MUSCULATURE OF THE RAT *

NORMAN W. VOGEL

IN HIS attempt to imitate gestational changes in the mouse vagina Schick [1] was able to produce artificially vaginal conditions similar to those of both early and late pregnancy by means of hormone injections and tissue implantations. Using increases in the circumference and weight of the vagina as his index of effect, he found conditions resembling those of *early* pregnancy with progesterone injections and with implantations, subcutaneous or into the vagina, of either corpora lutea or placentas. Testosterone was most successful in producing changes similar to those of *late* pregnancy in the vaginas of virgin mice. The increases in circumference which Schick observed in late pregnancy indicate relaxation of the vaginal musculature, the physiological control of which apparently has not been investigated. In the present series of experiments an attempt was made to determine what, if any, hormonal control is exerted over this muscle. The author is indebted to Dr. Alvalyn E. Woodward, under whose supervision this work was undertaken, for help and guidance. Owing to current conditions the continuance and completion of this work have necessarily been postponed indefinitely.

METHOD

It was decided that any changes in muscle tension produced by hormone extracts could best be observed by the suspension method, and it was found that they could be recorded on a kymograph by a delicate heart lever. White rats were used because their tissues were of a size more convenient to handle.

The entire vagina was removed from the sacrificed animal; the hair margin was taken as the outer limit and the hard tissue of the

* Contribution from the Department of Zoology, University of Michigan.

[1] Schick, R. D., "Experimental Simulation of Gestational Changes in the Vagina of the Mouse," *Journ. Morphol.*, **73**: 143–175. 1943.

cervix as the inner limit. The vagina was then cut across, into two equal loops of tissue and placed in warm Ringer-Tyrode solution. Effects on both loops, the inner or cervical portion and the outer portion, were recorded individually.

Each tissue "loop" was suspended between a lower hook formed of a fine vertical glass rod and another hook leading upward by a silk thread to a delicate heart lever. The whole suspension was immersed in a bath of Ringer-Tyrode solution at 37° C. and aerated through a capillary tube. Just sufficient fluid was used in the shell vial to immerse the tissue completely. Care was taken not to place undue tension on the tissue loop while recording any muscular contraction or relaxation. To accomplish this a writing point was carefully adjusted to trace upon a slow-moving lightly smoked kymograph drum.

Dosages of five international units of pitocin (Parke, Davis and Co.), or thirty rat units of theelin (Parke, Davis and Co., Aqueous Suspension), were added in each case to the 25 c.c. of saline bath solution. Placental extracts, which were also used, were made from fresh rat or hog placentas by cutting up the tissue and allowing it to stand in Ringer-Tyrode solution at least twelve hours under refrigeration. The filtered extract was of undetermined but relatively high concentration.

The effects of the various hormones and extracts to be tested were determined by placing them in the Ringer bath after the vaginal loop had been allowed to make a control record for about thirty minutes, during which time any normal relaxation would have taken place. From thirty minutes to one hour was allowed for any possible response to each dose.

Most of the virgin vaginas were taken in estrous stage, as determined by the vaginal smear technique. All pregnant vaginas were within one or two days of parturition.

RESULTS

Neither pitocin nor theelin alone had any apparent effect on the outer vaginal portion. However, a mild increase in tonus resulted with theelin in the inner or cervical portion of diestrous and estrous vaginas of virgin animals and in preparations made late in pregnancy. In some cases the injection of pitocin after theelin produced an additional increase in tonus, and in at least one or two a relatively

strong uterine-like contraction occurred immediately upon administration of this pituitary extract.

The most promising response, however, in respect to the phenomena which were of interest here resulted from the application of fresh placental extract (rat). A pronounced relaxation of both tissue loops of the preparations taken late in pregnancy occurred in a majority of the cases upon the addition of this material to the bath in unknown but relatively high concentrations. There may be some species-specific reaction here, for the addition of hog placental extract in two experiments did not duplicate and confirm these results, but, on the contrary, apparently produced contraction. However, as yet an insufficient number of experiments have been performed to make positive statements concerning this specificity.

SUMMARY

1. Pitocin alone had no effect on the tonus of the vaginal muscle of the white rat.

2. Theelin produced a slight tonic contraction in the inner or cervical half of vaginas from diestrous, estrous, and pregnant rats.

3. Pitocin administered after theelin stimulated the vaginal muscle to still greater contraction.

4. A saline extract of fresh rat placentas brought about pronounced relaxation of both inner and outer portions of vaginas taken from rats late in pregnancy.

MORE DATA ON DEPRESSION INDIVIDUALITY IN DOUGLAS LAKE, MICHIGAN *

PAUL S. WELCH

IN 1928 the writer published a paper dealing with certain limnological features of Douglas Lake, Michigan, in which depression individuality was definitely reported for the first time. Later (Welch and Eggleton, 1932, 1935) more data were added. In the meantime this phenomenon was found in certain multidepression lakes by other investigators. The peculiarly favorable structure of the Douglas Lake basin for this kind of investigation, the recognized importance of limnological researches extended over many seasons, and the challenge of associated problems led to the accumulation of still further data, a certain portion of which is presented here. The previously published data covered eighteen summers. Records for eight other summers are now added, making a total of twenty-six seasons. In no other lake has depression behavior been followed for so long a period. Since this series now seems adequate to exhibit the usual variations and other features of depression individuality in Douglas Lake, the writer expects to discontinue records of this sort except when necessity demands them in connection with other research projects.

The records given in the tables (Tables I–II) attached to this paper are selected from a larger number made during the progress of the work. For the most part the organization of the tables follows that of previous papers in order that comparisons may be facilitated. The field and laboratory methods were essentially those employed in the earlier work except that during recent seasons extensive use was made of a modern, sensitive electrical-resistance thermometer outfit constructed by the Foxboro Company. In all records thermocline limits were determined by the application of Birge's rule.

* Contribution from the Biological Station and the Department of Zoology, University of Michigan. This work was facilitated by a grant from the University of Michigan Faculty Research Fund.

The results from these last eight seasons, when compared with those of the preceding eighteen, are largely confirmatory. Well-defined individuality in the major depressions is consistently exhibited. Additions to the many details of depression performance have been made, but are of such a nature that they need not be listed here.

During the summers of 1938–42 many vertical temperature records were made from the various depressions on corresponding dates and at very close depth intervals, sometimes as small as 0.1 meter. One purpose of these series was to work out the detailed structure of the thermocline and to discover whether depression individuality extends also to the internal distribution of temperature. These voluminous records cannot be published here, but the principal result may be stated in very brief form. It was found that, when the successive values of fall in temperature from one level to the next lowest are plotted, the differences in internal structure of the thermoclines in the several depressions on the same or similar dates are made visible and easy to compare. From such graphs it is clear that, in addition to features stressed in earlier papers, depression individuality extends also to the internal structure of the thermocline.

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TABLE I

SUMMARY OF THERMAL STRATIFICATION IN DIFFERENT DEPRESSIONS

Date	Depth (meters)	Surface temp. (° C.)	Bottom temp. (° C.)	Thermocline	
				Depth limits (meters)	Temperature limits (° C.)
South Fish-Tail Depression (maximum depth, 24 meters)					
1934					
July 4	23	21.8	10.5	11–14	20.6–13.6
				16–17	13.0–11.7
July 25	23	25.0	10.5	12–16	20.2–12.8
Aug. 10	20	24.2	10.1	11–15	20.8–12.2
1935					
July 24	20	26.4	8.2	8–16	21.6–9.6
Aug. 14	22	24.3	8.2	10–16	20.8–9.6
1936					
July 11	20	29.1	9.2	4–7	25.0–20.2
				12–16	18.2–11.8
Aug. 7	20	22.0	9.8	12–17	20.4–11.4
1937					
July 12	23	27.0	9.6	8–9	19.4–18.1
				11–15	17.2–10.5
July 23	22	23.9	9.6	9–11	21.8–18.6
				13–14	17.2–12.8
July 28	22	19.8	9.6	15–17	18.8–11.6
Aug. 11	22	25.2	9.3	13–17	19.5–11.0
1938					
July 6	22	23.3	8.7	1–4	23.0–19.0
				11–13	15.3–12.6
July 22	21	22.0	10.0	10–16	20.3–12.0
July 29	21	22.1	10.4	11–15	20.7–13.5
Aug. 26	23	20.4	9.2	12–15	19.7–11.4
1939					
June 26	22	21.5	7.4	12–16	17.2–9.7
July 5	21	22.3	7.5	9–17	20.2–8.3
July 11	23	23.5	7.5	10–17.7	20.1–8.0
July 20	21	22.3	7.6	12–16.6	19.7–8.8
July 28	20	25.5	7.9	4–6	23.5–20.6
				12–16	18.1–7.5
Aug. 4	21	23.4	7.9	12–16	19.5–9.3
Aug. 14	21	23.2	7.8	11.6–16	20.4–9.2
1940					
June 26	22	16.1	6.9	14.5–17	14.7–8.0
July 3	20	18.4	7.1	14–17	15.2–7.9
July 17	20	19.0	7.1	9–10	17.7–16.1
				14–17	14.5–8.3

TABLE I (*Continued*)

Date	Depth (meters)	Surface temp. (° C.)	Bottom temp. (° C.)	Thermocline	
				Depth limits (meters)	Temperature limits (° C.)
South Fish-Tail Depression (*Concluded*)					
July 24	21	25.3	7.3	14–18	14.4–7.4
Aug. 15	21	23.2	7.3	8–10	20.2–17.8
				12–16.6	16.0–9.3
1941					
July 9	23	22.7	6.2	10–17	20.5–7.0
July 21	23	20.2	6.2	13–16	18.4–8.0
July 23	22	22.0	6.2	12–16	18.6–8.0
Aug. 9	20	25.0	6.5	12–18	19.0–8.0
1942					
July 8	22	19.2	7.0	11–16	17.5–9.0
July 31	23	23.3	7.2	10–16	21.2–9.4
Aug. 12	20	21.0	7.2	13–17	19.9–9.9
1943					
July 7	23	22.0	8.3	12–15	18.3–10.0
July 23	21	22.5	9.1	11–15	20.3–10.5
Aug. 18	21	20.0	9.0	13–16	19.4–10.0
Sedge Point Depression (maximum depth, 24 meters)					
1934					
July 3	22	22.0	11.4	11–12	20.8–19.3
				16–18	17.6–12.3
Aug. 6	23	22.2	11.6	15–18	20.7–13.6
1937					
Aug. 9	22	24.7	13.1	14–17	19.2–14.6
1938					
Aug. 25	25	21.3	12.3	14–16	19.9–13.7
1939					
June 29	22	23.5	12.5	5–6	20.9–19.7
				19–21.5	16.9–12.5
July 6	22	29.1	11.9	8–9	20.8–19.6
				17–20	16.8–12.9
July 17	20	21.4	13.7	13.5–18.4	18.4–12.5
Aug. 8	22	23.2	13.0	15.4–17	18.8–15.0
1940					
July 9	21	22.4	12.1	4–5	20.5–19.2
				17–18.2	15.5–13.1
July 26	21	24.6	12.8	4–9	23.7–18.1
				17–18	15.2–14.2
Aug. 15	22	22.7	12.7	8–10	20.6–17.5
1941					
Aug. 2	20	25.6	12.5	16–19	18.2–12.8

TABLE I (*Continued*)

Date	Depth (meters)	Surface temp. (° C.)	Bottom temp. (° C.)	Thermocline	
				Depth limits (meters)	Temperature limits (° C.)
Grapevine Point Depression (maximum depth, 25 meters)					
1934					
July 3	23	21.4	11.6	14–17	18.4–12.4
1937					
Aug. 9	22	22.0	12.8	14–17	18.6–13.9
1939					
June 27	24	21.4	17.3	5–6	21.1–19.5
July 6	24	24.7	16.7	No stratification	
July 18	24	22.0	16.7	14–15	19.7–18.3
Aug. 7	24	23.5	16.6	No stratification	
Aug. 16	24	24.4	16.5	14–15	20.3–19.0
1940					
July 4	23	18.7	10.2	3–4	17.9–16.8
				21–22	14.7–10.3
July 23	23	26.1	14.3	0–3	26.1–21.9
				5–9	20.7–17.1
Aug. 13	22	24.9	14.5	8–10	21.3–17.1
1941					
July 29	22	27.1	11.9	17–20	16.2–12.1
Stony Point Depression (maximum depth, 18 meters)					
1934					
July 5	19	22.5	13.6	13–17	19.9–13.6
Aug. 10	19	24.0	14.9	13–15	20.6–16.0
1937					
Aug. 9	17	24.0	18.9	No stratification	
1939					
July 19	18	21.7	17.2	16–16.5	19.6–17.7
1940					
July 23	16	26.6	14.0	1–3	25.7–21.5
				6–7	19.9–18.9
Aug. 13	18	25.8	15.9	7–10	21.2–17.3
1941					
Aug. 2	15	25.2	19.2	No stratification	
Roberts Point Depression (maximum depth, 22 meters)					
1934					
July 5	21	21.9	11.3	11–16	20.4–12.4

TABLE I (*Concluded*)

Date	Depth (meters)	Surface temp. (° C.)	Bottom temp. (° C.)	Thermocline	
				Depth limits (meters)	Temperature limits (° C.)
Roberts Point Depression (*Concluded*)					
1937					
Aug. 9	18.5	24.0	11.6	12–17	18.6–12.0
1938					
Aug. 25	22	21.0	12.0	12–13.7	19.6–13.7
1939					
June 29	19	24.4	11.3	2–4	24.1–20.5
				15–18.5	15.7–11.6
July 17	22	21.6	11.2	13–16	19.0–13.4
Aug. 10	20	23.5	12.3	11.4–17	21.1–13.3
1940					
July 9	19	23.7	10.2	3–4	20.8–18.1
				5–6	18.5–17.5
				15–18	15.4–10.3
Aug. 1	20	22.6	11.6	7–10	22.1–16.6
Aug. 17	20	25.3	13.4	9–12	22.5–17.6
1941					
July 29	19	27.3	8.8	11–17	18.9–9.7
Fairy Island Depression (maximum depth, 28 meters)					
1934					
July 2	26	21.4	12.2	13–15	17.4–13.8
Aug. 6	25	22.2	11.5	13–17	19.8–12.8
1937					
Aug. 11	24	24.6	11.5	13–16	18.5–12.5
1938					
Aug. 25	27	21.8	11.4	12–15	19.8–12.6
1939					
July 4	24	22.0	10.7	7–8	21.1–20.1
July 18	24	21.1	10.6	12–16	19.3–13.5
1940					
July 13	25	20.7	9.4	4–6	20.3–17.9
				15.6–18.4	14.8–10.6
Aug. 1	26	23.1	10.2	7–9	20.6–17.5
				16–17	13.7–12.7
Aug. 17	26	25.0	11.6	8–13	23.1–17.1
1941					
July 29	26	26.5	8.3	13–18	18.2–10.4

TABLE II

Summary of Chemical Analyses

Abbreviations: t. s., thermal stratification; t. gr., temperature gradient; c. s., chemical stratification; c. gr., chemical gradient (gradual quantitative change in chemical features from surface to bottom)

Date	Temperature conditions	Chemical conditions	Dissolved oxygen			Free CO_2		Methyl-orange alkalinity p.p.m.	pH	
			Surface and bottom cc./l	Thermocline cc./l	Oxygenless zone m.	Surface and bottom p.p.m.	Thermocline p.p.m.		Surface and bottom	Thermocline
South Fish-Tail Depression										
1934										
July 4	t. s.	c. s.	5.21–0.0	4.2 –2.56 1.68–0.73	19–23	0.0–7.0	0.0–1.0 3.0–4.0	108–124	8.2–6.9	8.2–7.7 7.3–7.2
July 25	t. s.	c. s.	3.95–0.0	1.56–0.0	16–23	0.0–7.0	1.0–5.0	120–138	8.2–6.9	7.8–7.0
Aug. 10	t. s.	c. s.	4.99–0.0	4.72–0.42	17–23	0.0–8.5	0.0–6.0	124–134	8.2–7.0	8.0–7.1
1935										
July 3	t. s.	c. s.	5.57–0.03	3.57–0.49	20–23	0.0–3.0	1.5–2.8	124–126	8.2–7.0	7.7–7.1
July 24	t. s.	c. s.	5.38–0.0	5.2 –0.63	18–23	0.0–4.0	0.0–2.5	130–142	8.4–7.0	8.0–7.4
Aug. 14	t. s.	c. s.	5.57–0.0	4.63–0.03	18–23	0.0–5.0	0.0–3.0	124–130	8.2–6.9	8.0–7.0
1936										
July 8	t. s.	c. s.	5.11–0.0	4.4 –0.82	21–23	0.0–6.0	1.0–4.0	102–130	8.0–7.0	7.8–7.1
Aug. 7	t. s.	c. s.	4.94–0.0	3.78–0.0	17–23	0.0–6.0	0.0–5.0	126–132	8.0–7.0	7.9–7.0
1937										
July 7	t. s.	c. s.	4.95–0.0	3.2 –1.7	19–23	0.0–5.0	1.0–3.5	125–136	8.0–7.1	7.8–7.2
July 23	t. s.	c. s.	5.4 –0.0	4.4 –2.8 1.4 –1.1	18–23	0.0–5.0	0.0–1.5 2.0–3.0	116–139	8.1–6.9	8.0–7.5 7.3–7.2
July 28	t. s.	c. s.	5.5 –0.0	4.6 –0.0	17–23	0.0–4.0	0.0–3.0	130–135	8.0–7.0	8.0–7.1
Aug. 11	t. s.	c. s.	5.6 –0.0	3.2 –0.0	17–23	0.0–10.0	1.5–10.0	130–142	8.2–7.0	7.7–7.2
1938										
July 6	t. s.	c. s.	5.34–0.0	5.34–5.34 3.0 –2.8	18–23	0.0–5.0	0.0–0.0 1.0–2.0	120–129	8.0–7.0	8.0–8.0 7.5–7.4

TABLE II (*Continued*)

Date	Temperature conditions	Chemical conditions	Dissolved oxygen			Free CO_2		Methyl-orange alkalinity p.p.m.	pH	
			Surface and bottom cc./l	Thermocline cc./l	Oxygen-less zone m.	Surface and bottom p.p.m.	Thermocline p.p.m.		Surface and bottom	Thermocline
South Fish-Tail Depression (*Concluded*)										
July 22	t. s.	c. s.	5.23–0.0	4.9 –0.23	18–23	0.0–5.0	0.5–3.0	116–134	8.2–7.0	7.8–7.1
July 29	t. s.	c. s.	5.26–0.0	3.4 –0.5	17–23	0.0–5.0	1.0–3.5	117–120	8.0–7.3	7.6–7.3
1939										
July 5	t. s.	c. s.	5.67–0.0	5.4 –0.06	18–23	0.0–4.0	0.0–3.0	107–114	8.3–7.0	7.9–7.1
July 11	t. s.	c. s.	5.13–0.13	4.3 –0.47	Absent	0.0–15.0	0.0–6.0	117–130	8.3–7.0	7.9–7.4
July 20	t. s.	c. s.	5.7 –0.0	4.6 –0.1	21–23	0.0–7.0	0.0–7.0	122–132	8.2–6.9	7.8–6.9
July 28	t. s.	c. s.	5.3 –0.0	3.2 –0.24	18–23	0.0–3.0	0.5–3.0	116–132	8.3–7.0	7.6–7.1
Aug. 4	t. s.	c. s.	3.8 –0.0	2.0 –0.1	17–23	0.0–14.0	1.0–8.0	115–141	8.2–6.9	7.5–7.0
Aug. 14	t. s.	c. s.	5.5 –0.0	2.9 –0.0	13.7–23	0.0–9.0	0.5–7.0	121–140	8.2–6.9	7.7–6.9
1940										
June 26	t. s.	c. s	6.1 –0.07	5.37–3.21	Absent	0.0–2.0	0.0–2.0	122–133	8.0–6.9	8.0–7.2
July 3	t. s.	c. s.	5.92–0.0	5.4 –0.2	20–23	0.0–10.0	0.0–10.0	119–133	8.2–7.0	8.0–7.0
July 17	t. s.	c. s.	5.72–0.0	5.6 –5.1	18–23	0.0–12.0	0.0–0.0	120–131	8.2–6.9	8.0–8.0
				5.3 –0.03			1.0–12.0			7.6–7.0
July 24	t. s.	c. s.	5.23–5.0	5.2 –5.7	19–23	0.0–12.0	0.0–0.0	118–131	8.2–7.0	8.2–8.2
				2.15–0.06			6.0–12.0			7.2–7.0
Aug. 15	t. s.	c. s.	5.43–0.0	5.5 –2.15	18–23	0.0–14.0	0.0–2.0	111–134	8.3–7.1	8.0–7.6
				1.83–0.03			3.0–10.0			7.5–7.1
1941										
July 9	t. s.	c. s.	5.43–0.0	4.54–0.34	20–23	0.0–10.0	0.0–7.0	120–132	8.4–7.0	8.2–7.0
July 23	t. s.	c. s.	5.63–0.0	4.63–0.6	19–23	0.0–12.0	0.0–7.0	121–131	8.4–7.0	7.9–7.1
Aug. 9	t. s.	c. s.	5.32–0.0	2.72–0.05	19–23	0.0–12.0	0.0–10.0	123–138	8.3–6.9	7.6–7.1
1942										
July 8	t. s.	c. s.	5.51–0.0	5.02–1.04	21–23	0.0–10.0	0.0–7.0	118–125	8.2–7.1	7.9–7.1
July 31	t. s.	c. s.	5.37–0.0	3.27–0.2	19–23	0.0–9.0	0.0–8.0	115–127	8.4–7.0	8.0–7.1
1943										
July 7	t. s.	c. s.	5.23–0.0	3.9 –2.72	20–23	0.0–10.0	3.0–5.0	116–130	8.2–7.2	7.8–7.3
July 23	t. s.	c. s.	5.3 –0.0	4.29–1.4	20–23	0.0–7.0	2.0–7.0	122–135	8.2–7.0	7.5–7.0
Aug. 18	t. s.	c. s.	5.71–0.0	4.88–0.69	17–23	0.0–7.0	0.0–5.0	124–124	8.2–7.0	7.8–7.2

TABLE II (*Continued*)

Date	Temperature conditions	Chemical conditions	Dissolved oxygen			Free CO_2		Methyl-orange alkalinity p.p.m.	pH	
			Surface and bottom cc./l	Thermocline cc./l	Oxygen-less zone m.	Surface and bottom p.p.m.	Thermocline p.p.m.		Surface and bottom	Thermocline
Sedge Point Depression										
1934										
July 3	t. s.	c. s.	4.48–0.0	2.42–0.73	19–25	0.0–5.0	1.0–2.0	110–134	8.2–6.8	7.4–7.0
Aug. 6	t. s.	c. s.	4.72–0.0	0.35–0.0	17–25	0.0–7.0	1.0–6.0	128–134	8.2–7.0	7.6–7.1
1937										
Aug. 9	t. s.	c. s.	5.5 –0.0	1.5 –0.0	17–25	0.0–13.0	4.0–9.0	129–142	8.2–7.1	7.4–7.2
1939										
June 29	t. s.	c. s.	6.2 –0.0	3.3 –0.1	22–25	0.0–6.0	2.0–6.0	116–129	8.2–7.0	7.4–7.1
July 6	t. s.	c. s.	5.6 –0.0	5.0 –4.6	23–25	0.0–5.0	0.0–0.0	123–132	8.2–7.0	8.2–8.0
				2.6 –0.75			2.0–5.0			7.4–7.2
July 17	t. s.	c. s.	5.4 –0.0	4.8 –0.61	22–25	0.0–5.0	0.0–4.5	116–122	8.2–7.3	8.1–7.3
Aug. 8	t. s.	c. s.	5.1 –0.0	0.41–0.0	16.7–25	0.0–7.0	4.0–5.0	121–137	8.2–7.1	7.2–7.1
1940										
July 9	t. s.	c. s.	5.48–0.0	5.4 –5.8	21–25	0.0–2.0	0.0–0.0	112–124	8.2–7.2	8.2–8.2
				3.8 –3.58			0.5–0.5			7.7–7.6
July 26	t. s.	c. s.	5.3 –0.0	5.5 –4.0	21–25	0.0–4.0	0.0–0.0	120–132	8.2–7.2	8.3–8.0
				2.21–1.87			2.0–2.0			7.4–7.3
Aug. 15	t. s.	c. s.	5.37–0.0	3.0 –2.1	17–25	0.0–7.0	0.0–1.0	115–133	8.3–7.1	8.0–7.7
1941										
Aug. 2	t. s.	c. s.	5.22–0.0	0.2 –0.0	19–25	0.0–10.0	7.0–10.0	114–136	8.4–7.1	7.2–7.1
Grapevine Point Depression										
1934										
July 3	t. s.	c. s.	5.28–0.0	2.49–0.29	20–25	0.0–9.0	3.0–6.0	102–136	8.2–6.9	7.5–7.0
1937										
Aug. 9	t. s.	c. s.	6.8 –0.0	2.18–0.03	18–25	0.0–14.0	3.0–8.0	114–136	8.2–7.2	7.5–7.2
1939										
June 29	t. s.	c. s.	5.6 –2.2	5.6–5.5	0	0.0–4.0	0.0–0.0	117–128	8.2–7.2	8.2–8.2
July 6	t. gr.	c. gr.	5.3 –0.9	No strat.	0	0.0–3.0	.....	126–126	8.2–7.2	.....

TABLE II (*Continued*)

Date	Temperature conditions	Chemical conditions	Dissolved oxygen			Free CO_2		Methyl-orange alkalinity p.p.m.	pH	
			Surface and bottom cc./l	Thermocline cc./l	Oxygen-less zone m.	Surface and bottom p.p.m.	Thermocline p.p.m.		Surface and bottom	Thermocline
Grapevine Point Depression (*Concluded*)										
July 18	t. s.	c. s.	5.7 –0.0	3.2 –1.5	23–25	0.0–7.0	2.0–3.0	116–128	8.2–7.1	7.4–7.3
Aug. 7	t. gr.	c. gr.	5.03–0.0	No strat.	22–25	0.0–5.0	.....	117–134	8.2–7.1	.....
Aug. 16	t. s.	c. s.	5.28–0.0	2.23–1.5	16–25	0.0–9.0	2.0–3.0	128–136	8.2–7.2	7.6–7.4
1940										
July 4	t. s.	c. s.	5.0 –0.65	5.0 –5.0 4.53–4.53	0	0.0–0.0	0.0–0.0 0.0–0.0	117–125	8.2–7.2	8.2–8.1 7.8–7.7
July 23	t. s.	c. gr.	5.0 –1.0	5.0 –5.2 5.5 –4.0	0	0.0–6.0	0.0–0.0 0.0–0.0	114–131	8.2–7.2	8.2–8.2 8.2–7.8
Aug. 13	t. s.	c. s.	5.85–0.0	4.9 –2.8	18–25	0.0–10.0	0.0–2.0	120–132	8.2–7.1	7.9–7.7
1941										
July 29	t. s.	c. s.	5.42–0.13	0.4 –0.13	0	0.0–10.0	6.0–10.0	124–140	8.4–7.1	7.1–7.1
Stony Point Depression										
1934										
July 5	t. s.	c. s.	5.35–0.0	3.3 –0.0	17–18	0.0–3.0	0.0–2.0	128–132	8.2–7.1	7.7–7.1
Aug. 10	t. s.	c. gr.	5.78–0.0	3.24–0.07	16–18	0.0–8.0	1.0–7.0	120–136	8.2–7.0	7.8–7.1
1937										
Aug. 9	t. gr.	c. gr.	6.0 –1.0	No strat.	0	0.0–7.0	.....	128–136	8.2–7.4	.....
1939										
July 19	t. s.	c. s.	5.5 –0.9	2.3 –1.9	0	0.0–3.0	1.0–1.5	124–122	8.2–7.2	7.4–7.4
1940										
July 23	t. s.	c. s.	5.57–2.01	5.57–5.6 5.8 –5.6	0	0.0–3.0	0.0–0.0 0.0–0.0	120–129	8.2–7.3	8.2–8.2 8.2–8.2
Aug. 13	t. s.	c. s.	5.37–0.06	5.24–0.36	0	0.0–6.0	0.0–4.0	115–131	8.2–7.2	8.0–7.3
1941										
Aug. 2	t. gr.	c. gr.	5.23–2.14	No strat.	0	0.0–3.0	.....	120–130	8.4–7.4	.....

TABLE II (*Continued*)

Date	Temperature conditions	Chemical conditions	Dissolved oxygen			Free CO_2		Methyl-orange alkalinity p.p.m.	pH	
			Surface and bottom cc./l	Thermocline cc./l	Oxygenless zone m.	Surface and bottom p.p.m.	Thermocline p.p.m.		Surface and bottom	Thermocline
Roberts Point Depression										
1934										
July 5	t. s.	c. s.	5.16–0.0	4.5 –1.54	19–22	0.0–4.0	0.0–2.2	120–132	8.2–7.0	8.0–7.3
1937										
Aug. 9	t. s.	c. s.	6.0 –0.0	3.4 –0.0	17–22	0.0–10.0	2.0–9.0	130–126	8.2–7.1	7.7–7.2
1939										
June 29	t. s.	c. s.	5.6 –0.6	5.7 –5.8 3.8 –0.4	0	0.0–5.0	0.0–0.0 1.0–5.0	117–129	8.2–7.0	8.2–8.2 7.5–7.0
July 17	t. s.	c. s.	5.6 –0.27	5.2 –1.2	0	0.0–8.0	0.0–2.5	116–124	8.2–7.1	8.0–7.3
Aug. 10	t. s.	c. s.	4.8 –0.07	4.7 –0.07	0	0.0–7.0	0.0–6.0	121–130	8.2–7.0	8.0–7.0
1940										
July 9	t. s.	c. s.	5.27–1.36	5.2 –5.4 5.6 –5.6 4.5 –1.9	0	0.0–1.5	0.0–1.5	120–125	8.2–7.2	7.8–7.3
Aug. 1	t. s.	c. s.	5.4 –0.7	5.4 –4.3	0	0.0–5.0	0.0–0.0	118–128	8.1–7.1	8.1–7.7
Aug. 17	t. s.	c. s.	5.3 –0.0	4.0 –1.5	18–22	0.0–10.0	0.0–4.0	116–128	8.2–7.1	7.8–7.4
1941										
July 29	t. s.	c. s.	5.23–0.0	4.56–0.1	18–22	0.0–12.0	0.0–11.0	129–134	8.3–7.0	8.1–7.0

TABLE II (*Concluded*)

Date	Temperature conditions	Chemical conditions	Dissolved oxygen			Free CO_2		Methyl-orange alkalinity p.p.m.	pH	
			Surface and bottom cc./l	Thermocline cc./l	Oxygen-less zone m.	Surface and bottom p.p.m.	Thermocline p.p.m.		Surface and bottom	Thermocline
Fairy Island Depression										
1934										
July 2	t. s.	c. s.	5.79–0.0	4.55–2.34	24–27	0.0–9.0	0.5–5.0	111–127	8.0–6.9	7.6–7.3
Aug. 6	t. s.	c. s.	5.77–0.0	4.5 –0.0	17–27	0.0–9.0	1.0–5.0	128–134	8.2–7.0	7.6–7.1
1937										
Aug. 11	t. s.	c. s.	4.9 –0.0	3.2 –0.1	18–27	0.0–10.0	3.0–9.0	128–130	8.2–7.1	7.6–7.2
1939										
July 4	t. s.	c. s.	5.7 –0.07	5.1 –4.8	25–27	0.0–6.0	0.0–0.0	120–124	8.2–7.0	8.1–8.0
July 18	t. s.	c. s.	5.6 –0.0	4.5 –0.8	19–27	0.0–9.0	0.0–4.0	114–121	8.2–7.0	7.9–7.1
1940										
July 13	t. s.	c. s.	5.33–0.0	5.36–5.56 4.02–1.94	26–27	0.0–7.0	0.0–0.0 1.0–2.5	117–127	8.3–7.0	8.3–8.3 7.7–7.2
Aug. 1	t. s.	c. s.	5.57–0.0	5.0 –3.3 1.5 –1.0	26–27	0.0–9.0	0.0–0.0 3.0–5.0	117–127	8.3–7.1	8.3–8.0 7.4–7.3
Aug. 17	t. s.	c. s.	5.3 –0.0	5.24–1.96	26–27	0.0–12.0	0.0–4.0	114–132	8.2–7.0	8.2–7.3
1941										
July 29	t. s.	c. s.	5.50–0.0	2.68–0.06	21–27	0.0–12.0	3.0–10.0	128–132	8.3–7.0	7.4–7.0

A STUDY OF THE SEDIMENT IN DOUGLAS LAKE, CHEBOYGAN COUNTY, MICHIGAN

IRA T. WILSON

IN ORDER TO study the sediment in Douglas Lake, located in Cheboygan County, Michigan, one hundred and eleven borings were made to the original bottom of the lake. Since an excellent contour map of the present basin (Fig. 1) was already available, the data secured from the borings were limited to the construction of contour maps of the original basin (Fig. 2), and of a later stage called the "high-level stage" (Fig. 3), and of profile diagrams (Fig. 4), which show the relationship of the original, high-level, and present basins to one another. The contour maps furnished the basis for determining the various morphometrical features (summarized in Table II) of the different basins as wholes and also for the many separate depressions for which the lake is notable.

Most of the borings were exploratory in the sense that they were made rapidly with the intention of discovering only the type of sediment and the depth of the transitional zones between the various kinds of sediment. Nine borings were made, however, in different parts of the lake from which complete cores of sediment were taken. These furnished a careful check on the conclusions based on the exploratory borings and gave material for the study of the chemical and petrographic nature of the sediment and the microfossils and laminations found in it. The fossil pollen from one boring (No. 74 in South Fish-Tail Bay, Fig. 1) has been examined and forms the subject of a paper already published (Wilson and Potzger, 1943). Dr. Ruth Patrick is studying the diatoms and Dr. Frank E. Eggleton the invertebrates from the cores; if the material warrants, they will make separate publications of it. The laminations in the sediment have proved profitable for the construction of a postglacial timetable, which will be the subject of still another paper in the near future.

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The writer is indebted to John McQuate and John H. Thompson, Jr., who helped do the field work during the summer of 1942 and made many of the computations in determining the morphometrical constants, and to Philip Krause and Howard Poetter, who assisted in the field work in 1943. He is very grateful to the staff of the Biological Station for many suggestions and much help, and especially to Dr. A. H. Stockard, who made the arrangements for the work, as well as to Drs. Paul S. Welch, Frank E. Eggleton, Frank C. Gates, and Gerald W. Prescott for suggestions and considerable assistance in the interpretation of the findings. Special acknowledgment of aid is due to Dr. A. S. Hazzard, director of the Institute for Fisheries Research, for his keen interest in the work and for his securing the means to carry it out.

Methods

The methods used in making the borings and taking the samples of sediment are substantially those described earlier by the writer (Wilson, 1941). He would like to add, however, that he learned that in working from a float on a good-sized lake where the water is rough a considerable part of the time, it is essential to have one as broad as the length of the maximum waves in order to avoid rocking.

A Brief History and Description of Douglas Lake

I. D. Scott (1921) describes Douglas Lake (Fig. 1) as having been "a depression in the bottom of one of the inlets of a great archipelago" during the existence of Lake Algonquin, and says that it became isolated as a separate body of water with the subsidence of the waters of Lake Algonquin. He continues his description as follows:

FIG. 1. Contour map of the present basin of Douglas Lake, showing the location of the 111 borings that form the basis of the maps of the original (Fig. 2) and high-level (Fig. 3) basins and the cross-section profiles (Fig. 4). It will be noted that (with few exceptions) the borings have been made along lines that cover the basin in all critical places. The lines are lettered (*A–A*, *B–B*, etc.) to correspond with the cross-section profiles in Figure 4. The names of the depressions can be determined by referring to Figure 2. The shoreline of this basin is 710 feet above sea level. The contours are taken from a map the contours of which were made by Dr. Paul S. Welch

The material surrounding the lake is all of glacial origin and is composed of sand, except at the headlands. These headlands are caused by till, which is much less readily attacked by the waves, and it will be seen from the map (Fig. 42) [1] that, in general, they are opposite each other. There seem to be two small till ridges here which cause the constrictions in the outline of the lake but do not persist across the basin unless possibly in the case of the more westerly. On either side and between the ridges are heavy deposits of sand which partially filled the depressions except where the lake now lies. The eastern end of the lake is surrounded by outwash but the sands of the central and western basins, although possibly outwash, were deposited, in part at least, on the bed of Lake Algonquin which formerly covered this region.

[1] The features referred to in this figure are also evident in Figure 1 of this paper.

The separate depressions found in Douglas Lake Scott assumed to be due to irregularities in one block of ice or to several separate blocks left by the melting ice sheet that had previously covered this region. This early period as an embayment of Lake Algonquin is referred to in this report as the Algonquin stage of the lake and the basin it occupied at the outset as the original basin. It was during this early period, according to Scott, that there was developed a broad terrace which still forms a conspicuous feature of the landscape

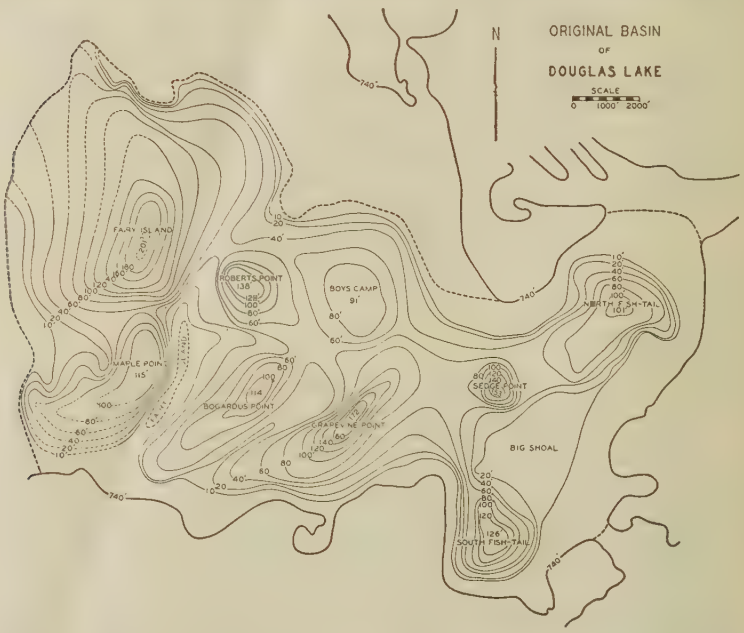

Fig. 2. Contour map of the original basin of Douglas Lake, showing the names and locations of the depressions. The data for the shoreline (where solid) were compiled from a topographical map of the Bogardus tract (southeastern end of lake) drafted by the College of Engineering and the School of Forestry and Conservation of the University of Michigan and from measurements and elevations (outside the Bogardus tract) made by the writer. The dotted part of the shoreline was drawn arbitrarily a little way outside the present shoreline in order to have a basis for determining the morphometrical constants of the original basin; such a procedure was necessary since it was this part of the original basin that was confluent with greater Lake Algonquin. The shoreline is 740 feet above sea level

around the lake at approximately the 730-foot elevation above sea level (about 20 feet above the present lake level). If it is assumed that 10 feet of water stood above this terrace when it was cut, then the Algonquin water level would have had an elevation of 740 feet. This is the basis on which the writer used the 740-foot contour (Figs. 1–2) as marking the original shoreline (Algonquin stage) of the lake.

Scott explains that, when the greater Algonquin Lake lowered to the Nipissing level and Douglas Lake became an isolated body of

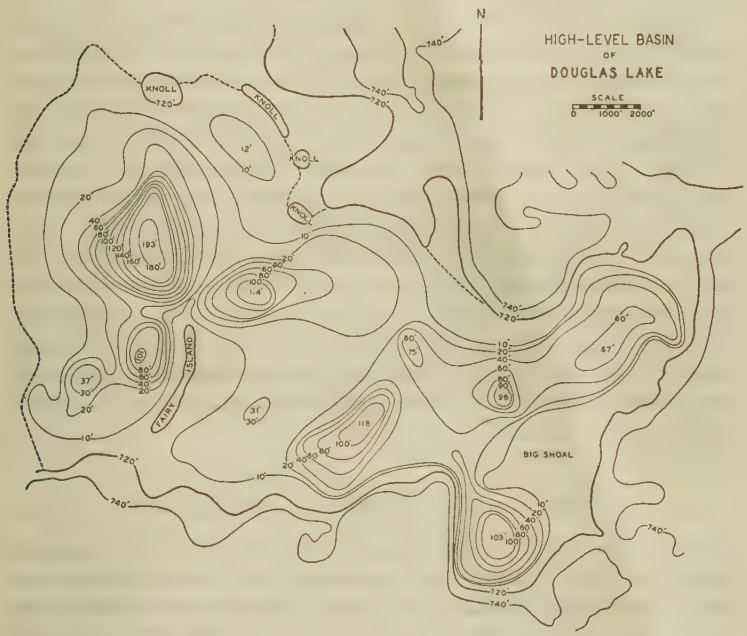

Fig. 3. Contour map of the high-level stage of Douglas Lake, that is, the basin at the end of the Algonquin stage. The depths were taken from the point of contact of the pink clay (Algonquin deposit) and black mud or marl (warm-water deposits). Data for the shoreline, which is 720 feet above sea level, were taken from a topographical map of the Bogardus tract (southeastern end of the lake) and measurements made by the writer. The dotted part of the shoreline was drawn arbitrarily just outside the present shoreline to form a basis for computing the morphometrical constants of the basin, since at this stage of the lake water covered several square miles of low sandy ground to the west and northwest which it did not seem practicable to include in this study

water, the surface of the lake was considerably higher than it is at present and that it was during this high-level stage that most of the shore adjustments were made that characterize the lake today. A broad wave-cut terrace about four feet above the present lake level was developed at this high-level stage. This terrace became exposed when the lake lowered to its present level, and if it is assumed that six feet of water stood above it, then the 720-foot contour can be used to mark the elevation of the water and shoreline for this stage of the lake, as was done in drafting Figures 1 and 3.

Welch (1927) and Welch and Eggleton (1932, 1935) have made special studies of the isolated submerged depressions that occur in Douglas Lake at the present time. There are seven such depressions, known as Fairy Island, Maple Point, Roberts Point, Grapevine Point, Stony Point, Sedge Point, and South Fish-Tail Bay (Fig. 2). The present study has revealed three additional depressions, now completely filled, as having existed in the past; they have been named Bogardus Point, Boys Camp, and North Fish-Tail Bay (Fig. 2). Undoubtedly these newly discovered depressions, like those known to Scott (1921), were caused by stranded blocks of ice from the receding Wisconsin ice sheet. Evidence will be submitted later suggesting that these dead blocks of ice remained in the several basins for varying lengths of time and thereby profoundly influenced the distribution of the sediment laid down during the early (Algonquin) stage of the lake.

Nature and Distribution of the Sediment

The sediment in Douglas Lake consists of four types, namely, gelatinous brown to black mud, marl, pink clay, and a brown varved clay. The gelatinous black mud forms the uppermost deposit and is soft for the first few feet, but becomes quite solid farther down and is almost like horn in the bottom reaches. The marl, which lies immediately below the black mud, is gray and rich in carbonates, being quite similar to that found at the surface in some lakes. Both the black mud and the marl are considered to be warm-water deposits (Fig. 4) and to have been laid down after Douglas Lake had become an isolated basin in which the water warmed and stratified in summer much as it does today; this would have been during the high-level and the present stages of the lake.

The pink clay is an amorphous deposit lying below the marl and is thought to have been made during the Algonquin period of the lake and, therefore, to have been a fairly cold-water deposit (Fig. 4). The fact that the water in Lake Algonquin probably had much of its source in the melting ice sheet implies the conclusion given above. The nearly complete lack of organic matter in the pink clay (Table I) and the fact that its color is due to the presence of iron oxide, which probably came from the iron deposits farther north, tend to confirm this interpretation.

The brown varved clay occurs in deposits about a foot thick in several localities in the lake basin below the pink-clay deposit. It was found near the surface at some places near shore, but was present below 104 feet of sediment (172 feet below the present water surface) at boring 2 (Fig. 1) in Fairy Island depression. Since this brown varved clay (often rather thick deposits) occurs over a wide area of this part of the State of Michigan, sometimes at levels higher than Lake Algonquin ever reached (Leverett and Taylor, 1915), it is likely that it antedates Douglas Lake. In Douglas Lake this deposit was always underlain with very fine sand that contains enough carbonates to give a vigorous reaction to hydrochloric acid. There was 41 feet of this fine sand lying under the brown clay at boring 42, below which is coarse gravel. If it should be ascertained that this clay layer is of earlier origin than the Algonquin stage of the lake, it could be utilized as a marker of the original bottom. This would remove some of the doubt expressed by the dotted lines on the map of the original basin (Fig. 2) and, consequently, reduce the volume of the original basin slightly.

That the sequence of deposits is not quite so simple as it appears from the foregoing description and the profile diagrams (Fig. 4), owing principally to the alternation of the various types of sediment at transitional zones between the major deposits, is shown by the following log of a core taken from the center of South Fish-Tail Bay depression: water, 72 feet; soft-flocculent black mud, 72–74 feet; gelatinous-laminated brown mud, 74–103 feet; gray marl, 103–106 feet; tough gelatinous-laminated black mud, 106–107 feet; gray marl, 107–108 feet; pink clay, 108–109 feet; sandy white clay, 109–109.5 feet; white and pink clay layers alternating, 109.5–112.5 feet; fine sand, 112.5–116 feet; sandy pink clay, 116–117 feet; dark-pink clay, 117–123 feet; sand, 123–123.5 feet; pink clay, 123.5–125 feet;

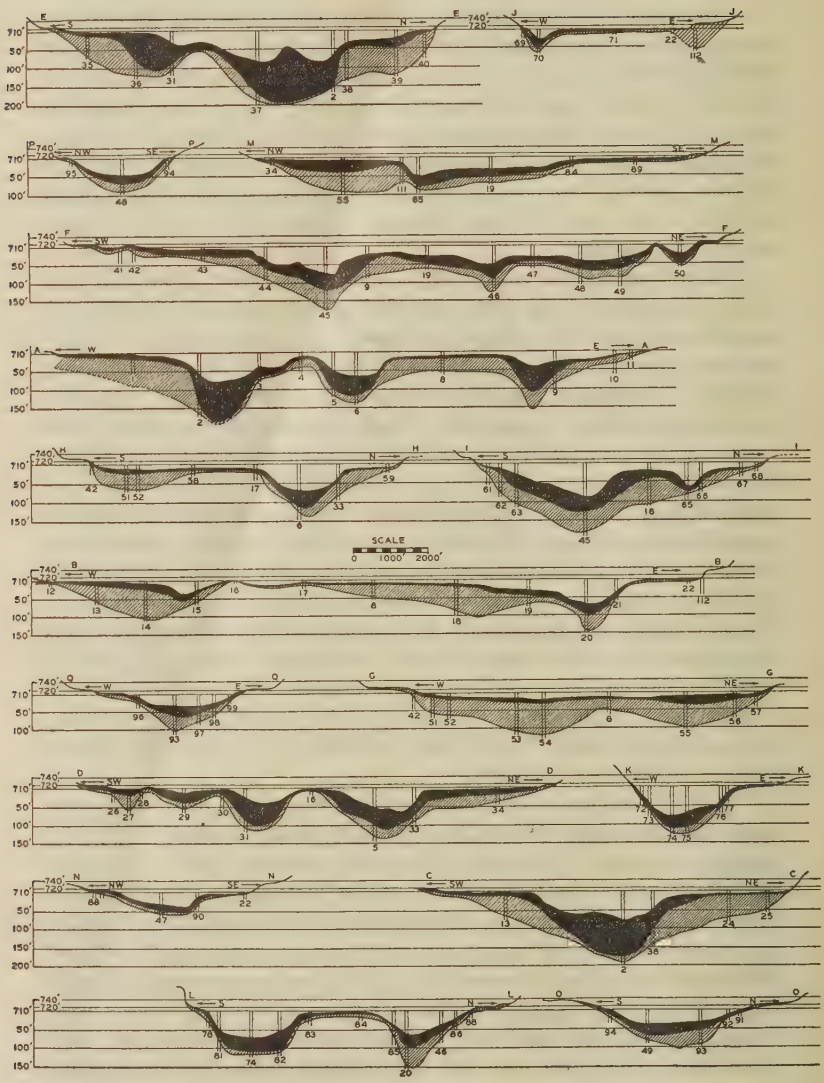

FIG. 4

(For the explanation of Figure 4 see the bottom of the facing page.)

sand, 125–126 feet; pink clay, 126–127 feet; sand, 127–127.5 feet; gray clay, 127.5–134 feet; fine sand, 134-135 feet; gray clay, 135–136 feet; fine sand, 136–137 feet; gray clay, 137–138 feet; coarse sand, 138–143 feet.

Table I gives a chemical and petrographic analysis for the four types of sediment listed above, namely, gelatinous black mud, gray marl, pink clay, and brown varved clay. The analyses were made by the laboratories of the Basic Refractories, Inc., of Tiffin, Ohio, to which the writer is indebted. The method of chemical analysis was that ordinarily used with limestone. Miss Elizabeth Haley, of the laboratory, who did the petrographic analyses, found it impossible to separate the material by the usual methods, owing to the large amount of calcite and organic matter present. She says: "No attempt was made to distinguish the various clay minerals — kaolin, dickite, sericite, etc. — and a complete identification of all minerals present was not undertaken." The analysis gives a good idea, however, of the relative abundance of the principal minerals.

The analysis of the black mud shows it to be mostly water (75 per cent). This is due to its gelatinous nature, because most of this water is an integral part of the jelly and cannot be removed by dehydration with alcohol. A sample taken from nearer the surface would have shown an even higher percentage of water. Exclusive of the water, a large part (30 per cent) of this sediment is organic matter in which pollen grains and fragments of plants can be recognized. Silicon dioxide makes up 48.80 per cent of this sediment (dry weight), which microscopic examination shows to be mostly the tests of diatoms. Quartz, calcite, and limonite were recognized in the petrographic analysis, their importance being in the order given.

The marl sample analyzed, although appearing to be no firmer than the gelatinous sediment, contained only 47.99 per cent of water. On the basis of dry weight there are considerable quantities of organic

EXPLANATION OF FIGURE 4

Cross-section profiles, showing the relationship of the basins of the three stages of Douglas Lake. The bottom line represents the original basin; the middle line (border crosshatched and black), the high-level basin; and the top line, the present basin. The crosshatched areas indicate the pink-clay deposit of the Algonquin stage, and the shaded portion (warm-water deposit) represents the marl (lower part usually only a few feet) and black mud that accumulated during the high-level and present stages. The locations of these cross sections are given in Figure 1

matter (11.30 per cent) and silicon dioxide (27.20 per cent). The carbonates (mostly calcium and magnesium) form a large proportion of the sediment (approximately 50 per cent), mostly in the form of calcite and dolomite. There was a small quantity of kaolins, also.

By dry weight the pink clay is 48.20 per cent silicon dioxide,

TABLE I

Analyses of Selected Samples from Boring 74 in South Fish-Tail Bay Depression

Sample composition	Gelatinous black mud	Marl	Pink clay	Brown varved clay (near Burt Lake)
Depth of water (feet)	69	69	69	15 (above surface)
Depth below water surface (feet)	77–94	98–99	109–110	15 (above surface)
Chemical constituents (Percentage — dry weight)				
SiO_2	48.80 (Diatoms)	27.20	48.20 (Quartz)	38.34
R_2O_3	6.00	6.00	12.36	10.85
CaO	4.20	24.00	9.55	15.35
MgO	1.30	3.80	7.84	8.14
Loss on ignition	35.00	34.35	16.60	21.68
Calculated amount of organic matter	30.00	11.30	1.00	None
Petrographic analyses				
Color of wet samples	Black	Grayish green	Brown	Pinkish tan
Color of dry samples	Gray green	Gray	Tan	Pinkish tan
Color after leaching with HCL	Brownish gray	Dark olive green brown when dried		Blue gray
Loss of water on drying	75.00 %	47.99 %	34.24 %	Large quantity
Names of minerals	Quartz *	Calcite *	Dolomite *	Dolomite *
	Calcite	Dolomite	Clay	Calcite
	Limonite	Kaolins	Quartz	Kaolins
		Quartz	Feldspar	Quartz
		Limonite	Iron oxide	Limonite
		Feldspar	Titanite (?)	Feldspar
			Zircon (?)	Titanite (?)
				Zircon (?)

* In order of abundance.

nearly all in the form of quartz. The percentage of magnesium oxide is higher than in the marl, and that of calcium oxide is lower; these minerals occur mostly in the form of dolomite. The R_2O_3 compounds are more abundant, probably owing to the increase in aluminum oxide found in the higher proportions of clay and feldspar present. The iron oxide in this sediment undoubtedly accounts for its characteristic pink color. The large amount of clay causes the physical appearance of the sediment. Organic matter constitutes only 1 per cent and, therefore, is almost entirely absent from this material; it is made up to some extent of pollen grains.

The brown varved clay is much like the pink clay, except that considerable calcite as well as limonite is present; the limonite accounts for the brown color. The number of varves ranges from 10 to 30 per inch, and they indicate that the deposit was laid down in cold water, since they do not form in water over 10 degrees centigrade.

The distribution of the warm- and the cold-water types of sediment is indicated on the profile drawings (Fig. 4). The black shaded portions of the profiles represent the gelatinous black mud and the marl; the marl makes up only a few feet of this part of the deposit near the bottom. The crosshatched portion of the profiles indicates the pink-clay deposit. By means of graphs, Figure 5 gives a good idea of the distribution of the sediment in the various separate depressions and in the lake as a whole.

Morphometrical Changes in the Basins

1. Introduction

Reference has been made to the fact that Douglas Lake has passed through three stages, namely, (1) the Algonquin, at which time it formed an embayment in the great postglacial Lake Algonquin, (2) the high-level stage, which began when Lake Algonquin receded to the Nipissing level and isolated the Douglas Lake embayment, and (3) the present stage, which is approximately ten feet lower than the high-level stage. There is no way to distinguish between the sedimentary deposits laid down during the high-level and the present stages; consequently the comparisons between stages are between the basins of the beginning of the Algonquin stage (original basin), of the beginning of the high-level stage (high-level basin), and of today. At the west end of the lake the study of the morphometry of the

original and high-level basins has been restricted to the region of the present basin, in spite of the existence of a broad contiguous plain extending several miles beyond that was covered with water during the Algonquin and high-level stages. The character of the deposit over this plain indicates that it resulted more from forces within the main body of Lake Algonquin than from the forces prevailing within the embayment that subsequently formed Douglas Lake.

In this section of the report four things will be described: (1) the three stages of each depression (with a comparison of similar morphometrical features included); (2) the three stages of the lake as a whole; (3) certain boulder belts; and (4) unusual sand deposits found in some depressions. The morphometrical data for all the depressions and for the lake as a whole are tabulated in Table II, together with the percentages of change that took place between the stages. It should be kept in mind that in the morphometrical computations each depression was considered as if the topmost complete contour (isolation contour) were its shoreline and marked the surface level of the depression. Obviously, from this point of view, all the depressions were submerged many feet below the general surface water of the lake and, consequently, were removed from the influences of wave action. No other way to work out the morphometrical features for purposes of comparison seemed feasible.

2. DESCRIPTIONS OF THE DEPRESSIONS AND COMPARISON OF THE MORPHOMETRICAL FEATURES OF THE THREE STAGES

Fairy Island depression. — This depression (Figs. 1–3) is by far the largest of all the depressions in Douglas Lake at all three stages, as is indicated by the areas at the various isolation contours (60 feet for the original basin; 50 feet for the high-level; and 40 feet for the present basin). The original Fairy Island depression has an area of 27,590,000 sq. ft., the high-level stage 9,063,000 sq. ft., and the present basin 7,042,000 sq. ft. This is a decrease of 67.15 per cent from the original to the high-level stage and of 22.30 per cent from the high-level to the present stage. Such a marked decrease in area from the original to the high-level basins indicates a tremendous accumulation of sediment around the periphery of the basin during the Algonquin stage.

The data given above and all other data referred to in this section will be found in tabular form in Table II.

The maximum depth of Fairy Island depression increased from 141 to 143 feet from the original to the high-level stage and the mean depth from 46.44 to 69.35 feet, which shows that scarcely any of the sediment settled in the center of the basin during Algonquin time. In great contrast there was a decrease of 66.72 per cent (from 69.35 to 23.08 feet) in mean depth after the beginning of the high-level stage; these changes, together with the rather small decrease in area (22.30 per cent), indicate that practically all the sediment settled in the center of the basin during this time. By looking at the graph (Fig. 5) the changes noted above can be visualized.

The reduction in volume from the original (1,281,430,000 cu. ft.) to the high-level (628,599,000 cu. ft.) stage was 50.94 per cent as contrasted with a reduction of 74.14 per cent from the high-level to the present stage (162,567,000 cu. ft.). The absolute amounts of the reductions in volume were 652,831,000 and 466,032,000 cu. ft., respectively.

In view of the contrasting changes in area and maximum and mean depths during the Algonquin and subsequent stages of the lake, it is not surprising to find that the mean slope increased from 5.19 to 11.95 per cent during the former period and decreased from 11.95 to 5.92 per cent during the latter one.

There was an increase in volume development of 40.00 per cent from the original (1.0) to the high-level (1.4) basins. In contrast to this there was no change from the high-level (1.4) to the present (1.4) basins.

The length of the shoreline decreased from the original (21,250 feet) to the high-level (11,750 feet) basin by 44.70 per cent but increased by 13.19 per cent from the high-level to the present (13,300 feet) basin. Shore development did not change during the Algonquin stage but increased 27.27 per cent (1.1 to 1.4) during the subsequent period. These figures are significant so far as the original to high-level changes are concerned, but are not so dependable in comparing the high-level to the present basin because the "shoreline" (isolation contour) of the present basin was determined from so many more soundings than those of the other two basins were that it shows many irregularities overlooked in the two earlier basins.

The volume of sediment (Table III) laid down during the Algonquin stage was 836,101,000 cu. ft. and that laid down subsequently, that is, since the beginning of the high-level stage, is 546,560,000

TABLE

SUMMARY OF ALL MORPHOMETRICAL

All morphometrical computations for the depressions were made as if the top- order to make comparisons more meaningful for the lake as a whole the maximum the surface of the present basin marked the surfaces of all three stages.

NAME OF DEPRESSION	AREA (Square feet)			MAXIMUM DEPTH (Feet)		
	Original	High level	Present	Original	High level	Present
Fairy Island	27,590,000	9,063,000	7,042,000	141	143	49
		−67.15*	−22.30*		+1.42	−65.73
% of change		−74.46*			−65.25	
Grapevine Point	9,192,000	6,799,000	3,936,000	102	88	51
		−26.03	−42.04		−13.72	−42.05
% of change		−57.17			−50.00	
Boys Camp	6,737,000	0.0	0.0	31	0.0	0.0
		−100.00	0.0		−100.00	0.0
% of change		−100.00			−100.00	
Maple Point	6,412,000	1,886,000	637,000	55	51	11
		−70.57	−66.25		−7.27	−78.43
% of change		−90.06			−80.00	
North Fish-Tail Bay	5,473,000	3,732,000	1,503,000	41	17	4
		−31.81	−59.73		−58.54	−76.47
% of change		−72.54			−90.24	
Bogardus Point	4,859,000	7,459,000	1,920,000	64	11	9
		+74.09	−74.26		−82.81	−18.18
% of change		−60.49			−85.94	
Roberts Point	3,906,000	11,897,000	3,880,000	78	94	52
		+204.66	−67.38		+20.51	−44.68
% of change		−0.64			−33.33	
South Fish-Tail Bay	2,663,000	4,522,000	3,926,000	56	63	43
		+69.78	−13.17		+12.50	−31.75
% of change		+47.40			−23.21	
Sedge Point	1,681,000	2,426,000	1,835,000	83	46	39
		+44.31	−24.37		−44.58	−15.22
% of change		+9.13			−53.01	
Stony Point	0.0	725,000	701,000	0.0	25	19
		0.0	−3.24		0.0	−24.00
% of change		0.0			0.0	
Whole lake	199,465,000	173,458,000	160,088,000	201	193	89
		−13.04	−7.71		−3.98	−53.89
% of change		−19.74			−55.72	

* These figures and others in the same relative position represent the percentage of change for the figures between which they lie.

II

DATA FOR DOUGLAS LAKE

most complete contour of a depression were the "surface" of the basin. In depth, mean depth, volume development, and mean slope were calculated as if

MEAN DEPTH (Feet)			VOLUME (Cubic feet) †		
Original	High level	Present	Original	High level	Present
46.44	69.35	23.08	1,281,430,000	628,599,000	162,567,000
	+49.33	−66.72		−50.94	−74.14
		−50.30			−87.31
29.18	35.73	18.80	268,235,000	242,918,000	74,037,000
	+22.45	−47.38		−9.44	−69.52
		−35.57			−72.40
16.65	0.0	0.0	112,248,000	0.0	0.0
	−100.00	0.0		−100.00	0.0
		−100.00			−100.00
27.76	25.83	5.86	188,022,000	48,736,000	3,739,000
	−6.95	−77.31		−74.08	−92.33
		−78.89			−98.01
21.45	15.35	1.33	117,428,000	31,107,000	2,004,000
	−28.45	−91.33		−73.51	−93.56
		−93.80			−98.29
20.01	5.26	7.59	107,278,000	39,242,000	14,578,000
	−73.71	+44.30		−63.42	−62.85
		−62.07			−86.41
29.02	25.26	29.92	113,361,000	300,599,000	116,167,000
	−12.96	+18.49		+165.17	−61.35
		+3.08			+2.47
32.00	37.17	24.25	85,260,000	168,099,000	95,223,000
	+16.16	−34.76		+97.16	−43.35
		−24.22			+11.68
33.50	16.76	16.45	56,326,000	40,660,000	30,186,000
	−49.97	−1.84		−27.81	−25.76
		−50.90			−46.41
0.0	10.19	6.93	0.0	7,386,000	4,859,000
	0.0	−32.00		0.0	−34.21
		0.0			0.0
47.87	28.64	18.17	14,942,574,000	6,634,224,000	2,908,403,000
	−40.19	−36.59		−55.60	−56.16
		−62.03			−80.54

† The detailed tables showing the volumes by frusta are on file in the Institute for Fisheries Research at Ann Arbor, Michigan.

TABLE

Name of Depression	Volume Development			Mean Slope (Percentage)		
	Original	High level	Present	Original	High level	Present
Fairy Island	1.0	1.4	1.4	5.19	11.95	5.92
		+40.00	0.0		+130.25	−50.46
% of change		+40.00			+14.02	
Grapevine Point	0.9	1.2	1.1	7.08	7.99	6.07
		+33.33	−8.33		+12.85	−24.03
% of change		+22.22			−14.26	
Boys Camp	1.6	0.0	0.0	2.32	0.0	0.0
		−100.00	0.0		−100.00	0.0
% of change		−100.00			−100.00	
Maple Point	1.5	1.5	1.6	6.25	8.05	2.78
		0.0	+6.67		+28.80	−65.46
% of change		+6.67			−55.52	
North Fish-Tail Bay	1.6	2.7	1.0	4.50	1.78	0.99
		+68.75	−62.96		−60.44	−44.32
% of change		−37.50			−78.00	
Bogardus Point	0.9	1.4	2.5	6.34	0.51	1.87
		+55.56	+78.57		−91.89	+264.78
% of change		+177.78			−70.23	
Roberts Point	1.1	0.8	1.7	7.93	4.77	6.84
		−27.27	+112.50		−38.85	+43.40
% of change		+54.54			−13.73	
South Fish-Tail Bay	1.7	1.8	1.7	8.92	8.01	6.55
		+5.88	−5.65		−10.20	−18.23
% of change		0.0			−26.57	
Sedge Point	1.2	1.1	1.3	13.49	5.49	6.55
		−8.33	+18.18		−59.30	+19.31
% of change		+8.33			−51.44	
Stony Point	0.0	1.2	1.1	0.0	5.72	4.55
		0.0	−8.33		0.0	−20.45
% of change		0.0			0.0	
Whole lake	0.7	0.5	0.6	5.89	3.72	2.81
		−28.57	+20.00		−36.86	−24.44
% of change		−14.29			−52.29	

II (*Continued*)

Length of Shoreline (Feet) (Isolation contours)			Shoreline Development			Average Depth of Sediment§ (Feet)			Isolation Contour		
Original	High level	Present	Original	High level	Present	Original high level	High level present	Original present	Original	High level	Present
21,250	11,750	13,300	1.1	1.1	1.4	30.30	60.30	53.10	60	50	40
−44.70	+13.19		0.0	+27.27							
−37.41			+27.27								
14,100	10,450	9,000	1.3	1.1	1.3	37.55	24.84	49.68	70	30	30
−25.89	−13.87		−15.38	+18.18							
−36.17			0.0								
9,800	0.0	0.0	1.1	0.0	0.0	15.18	0.0	15.18	60	0	0
−100.00	0.0		0.0	0.0							
−100.00			0.0								
11,850	5,100	4,950	1.3	1.0	1.7	28.19	30.53	39.73	60	50	40
−56.96	−29.41		−23.08	+70.00							
−58.23			+30.77								
10,100	9,100	7,450	1.2	1.3	1.7	24.18	29.30	33.83	60	50	40
−9.90	−18.13		+8.33	+30.77							
−26.24			+41.67								
10,250	11,500	8,000	1.3	1.2	1.6	52.03	11.56	59.08	50	20	10
+12.19	−30.43		−7.93	+33.33							
−21.95			+23.08								
7,400	14,600	8,300	1.1	1.2	1.2	32.98	15.50	39.15	60	20	20
+97.30	−43.15		+9.09	0.0							
+12.16			+9.09								
6,300	10,300	9,100	1.1	1.4	1.3	9.36	25.46	45.74	70	40	30
+63.49	−11.65		+27.27	−7.14							
+44.44			+18.18								
5,300	5.900	5,800	1.2	1.1	1.2	33.75	13.10	46.91	70	50	40
+11.32	−1.69		−8.33	+9.09							
+9.43			0.0								
0.0	3,800	4,400	0.0	1.3	1.5	0.0	13.32	0.0	0	50	40
0.0	+15.78		0.0	+15.38							
0.0			0.0								
‡	‡	74,400	‡	‡	1.6	22.97	11.86	33.29	−30	−10	0
0.0	0.0		0.0	0.0							
0.0			0.0								

‡ So much of the original and high-level shorelines was drawn arbitrarily that it makes futile a computation of their length and of their development.

§ The volume of sediment in each depression was computed as if the lower basin of any two lake stages, e.g., the original and the high level, included a special frustum extending from the topmost contour of the lower to the level of the topmost contour of the upper basin. In computing the *average depth of sediment* the total value for the quantity of sediment was always divided by the area of the topmost contour of the lower of the two basins being considered.

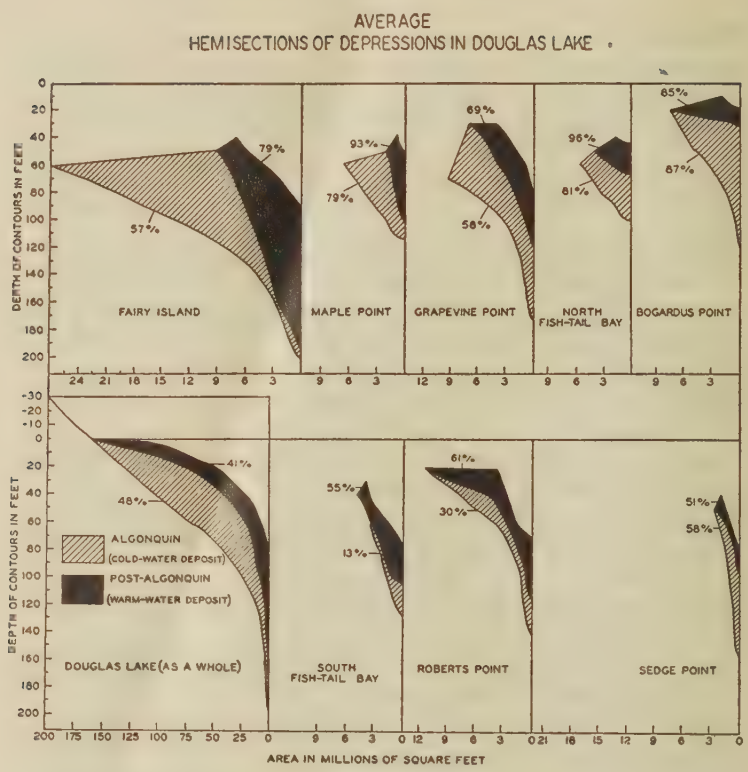

FIG. 5. Graphs made by plotting the areas within the various contours of the different stages of the depressions and the lake as a whole against the depths of the contours. They can be taken to represent average half cross sections of the depressions. The areas of the graphs between the curves for the different basins represent sediment. The graphs help one to visualize the parts of the basins in which the sediment accumulated at different stages as well as the changes in slopes, maximum depths, and other things. The percentages indicate the amount of filling of the basin in which they occur

cu. ft. Comparison of tables giving the volume of sediment by frusta (on file at the office of the Institute for Fisheries Research) shows that 50 per cent of the sediment laid down during the Algonquin stage lies above the base of the third frustum (30-foot contour), whereas 50 per cent of that deposited afterward (high-level and pres-

ent stages) lies above the base of the sixth frustum (60-foot contour). This difference follows from the fact that most of the sediment was laid down in the shallow periphery of the basin during the Algonquin stage but in the center during the later stages.

Maple Point and Grapevine Point depressions. - These two depressions resemble Fairy Island depression in that most of the pink-clay sediment characteristic of the Algonquin period of the lake settled around the periphery of the basin, whereas the reverse process (filling in the center) prevailed during the high-level and the present stages of the lake. This sequence of filling caused changes in the morphometrical features, from the original to the high-level stage on the one hand and from the high-level to the present stage on the other, to be about the same as those for the corresponding periods in Fairy Island depression. These resemblances can be verified by consulting Table II. Figure 5 shows the similarities graphically.

The three basins described so far, namely, Fairy Island, Maple Point, and Grapevine Point, were the largest and had the greatest maximum depth and volume of all the ten depressions in the original basin of Douglas Lake. They must have been formed by the largest blocks of ice. Their size, as will be shown later, probably is responsible for the peculiar manner in which they were filled as contrasted with that of the other basins.

Bogardus Point depression. — This depression differs radically from those already described in that it was almost completely filled with pink clay during the Algonquin stage of the lake. The difference is reflected to some extent in changes that have taken place in morphometrical features (Table II). During the Algonquin stage sediment settled in the center more rapidly than around the periphery (Fig. 5) and thus caused a reduction in maximum depth from 64 feet in the original basin to 11 feet in the high-level basin and a reduction in mean depth from 20.01 to 5.26 feet. An increase in area by 74.09 per cent (from 4,859,000 to 7,459,000 sq. ft.) from the original to the high-level basin emphasizes the fact that there was relatively little filling in of sediment around the edges of the basin. This is shown, also, by the accumulation of 84 feet of sediment in the center of the depression (boring 53), whereas the topmost contour (isolation contour) was raised only 30 feet during the Algonquin period. The reduction in volume (63.42 per cent) was likewise considerably greater than that in the Fairy Island depression, where the filling

was largely around the periphery during the same period. A reduction of 91.89 per cent in mean slope (from 6.34 to 0.51 per cent) during this period follows from the increase in area and the reduction in depth. Some decrease in irregularity in the shoreline is shown by the decrease in shoreline development from 1.3 to 1.2 per cent.

Owing to the more rapid accumulation of sediment around the periphery than in the center of the basin, shown by the reduction of 74.26 per cent in area and the relatively slight reduction in maximum depth of 18.18 per cent, the morphometrical changes in this depression during the time subsequent to the Algonquin period (the period of the high-level and the present basins) are of a kind diametrically opposite to those that took place from the original to the high-level basin. The volume was reduced by 62.85 per cent. The rate of reduction in area, which was faster than that in maximum depth, caused an increase in mean slope from 0.51 to 1.87 per cent.

The present basin of Bogardus Point depression is in reality only an embayment, but the mouth of the bay was arbitrarily taken as the limit of the lakeward side of the basin.

It is evident that Bogardus Point depression filled in a manner exactly opposite to that of Fairy Island, Maple Point, and Grapevine Point depressions at corresponding periods.

Boys Camp depression. — It is impossible to learn whether or not the filling of this basin took place more rapidly around the periphery than in the center, since the basin was completely obliterated during the Algonquin stage of the lake, but it undoubtedly did fill in the center at a rapid rate, which puts the basin in the same class as Bogardus Point depression during the Algonquin period. No filling has occurred since the Algonquin stage.

South Fish-Tail Bay depression. — Uniquely, no appreciable amount of sediment settled around the periphery, and very little did so in the center in the Algonquin stage of this depression (Fig. 5). The change in the isolation contour from 70 to 40 feet between the original and the high-level stages makes a deceiving situation, since it suggests considerable filling around the edge, but the 30-foot elevation is due to the plugging of a narrow channel connecting the depression to the main body of the lake (compare Figs. 2–3) and not to deposition within the basin itself. This elevating of the isolation contour is chiefly responsible for the increase in area (69.78 per cent),

maximum depth (12.50 per cent), mean depth (16.16 per cent), and volume (97.16 per cent). Since the area increased more than the maximum depth, the mean slope shows a decrease (10.20 per cent). Volume development, length of shoreline, and shoreline development also increased. The mean depth of sediment which accumulated during this period was only 9.36 feet, which is less than one third of the average amount that accumulated in the other nine basins during the same time (Table II).

In sharp contrast to the morphometrical changes that occurred during the Algonquin stage every morphometrical feature shows a decrease in value from the beginning of the high-level stage. The average depth of sediment accumulated during this later period is 25.46 feet. Most of it settled in the central deep part of the depression (Fig. 5), which is shown by the facts that there was only a 10-foot elevation in the isolation contour and that the maximum depth decreased 31.75 per cent.

North Fish-Tail Bay depression. — Since about the same amount of sediment accumulated around the periphery as in the center, both during the Algonquin stage and subsequently (Fig. 5), North Fish-Tail Bay depression might be taken as the mean of the ten depressions. The justification for this conclusion is found in the morphometrical changes (Table II) that took place during the two periods; they are all negative except volume development and shoreline development, both of which increased between the original and the high-level stages. For example, between the original and the high-level stages the area decreased 31.81 per cent, maximum depth 58.54, mean depth 28.45, volume 73.51, mean slope 60.44, and length of shoreline 9.90. The average depth of the sediment that formed here is 24.18 feet. The corresponding figures for the changes from the high-level to the present stage are considerably greater; they show acceleration in the same trends, which is undoubtedly due to the greater relative quantity of sediment that accumulated during this time, namely, an average of 33.83 feet.

Stony Point depression. — This depression formed an arm of Grapevine Point depression during the Algonquin period (Fig. 2) but was cut off as an independent depression as early as the time of the high-level stage by a ridge of sediment that formed across the base of the arm (Fig. 3). During the high-level and the present stages of the lake there has been a fairly uniform accumulation of sediment

over the entire basin, which has reduced moderately the area, maximum depth, mean depth, volume, slope, and volume development (Table II). The length of shoreline and the shoreline development increased slightly. These changes are very much like those that occurred in North Fish-Tail Bay depression during the same period. The average depth of sediment deposited is 13.32 feet.

Roberts Point depression. — The striking feature about Roberts Point depression is that between the original and the high-level basins it shows, among all the depressions, the greatest change in elevation of its isolation contour (from 60 to 20 feet), owing to the damming of the basin at the southeastern and northwestern corners rather than to an accumulation of sediment around the periphery (compare Figs. 2–3). These changes caused the greatest relative increase in area in all the depressions (204.66 per cent). This increase was partly because most of Boys Camp depression became incorporated with it by the time the high-level stage had been reached. There was an increase in maximum depth of 20.51 per cent, which is the greatest increase in depth that took place in all the depressions. The fact that the area increased more than the volume and the maximum depth caused decreases in mean depth (12.96 per cent) and mean slope (38.85 per cent). The volume increased by 165 per cent. The volume development decreased 27.27 per cent. This gave the high-level basin the lowest value in volume development (0.8) in all depressions at any stage. Length of shoreline and shoreline development both increased (97.30 and 9.09 per cent). About an average amount of sediment (23 feet at boring 6) settled in the center of the basin during the Algonquin stage.

From the high-level to the present basin every morphometrical feature changed in a manner opposite to that noted above for the changes from the original to the high-level stage (Table II). Fifty-one feet of sediment accumulated during this period at the point where boring 6 was made. That most of the sediment accumulated in the center of the depression during this period is shown also by the lack of any elevation in the isolation contour.

Sedge Point depression. — Of all the depressions this one was originally the smallest in area, volume, and length of shoreline, but it was one of the deepest (83 feet maximum depth from the isolation contour). The small area and the great depth account for the unusual steepness of its mean slope (13.49 per cent). It filled rather

slowly around the periphery but rapidly in the center during the Algonquin stage (Fig. 5). The depression increased in area (44.31 per cent) and decreased in maximum depth (44.58 per cent) and mean slope (59.30 per cent). The length of shoreline increased 11.32 per cent. Volume decreased (27.81 per cent), as did volume development (8.33 per cent) and shoreline development (8.33 per cent).

During the high-level and the present stages of Sedge Point depression sediment settled slightly faster around the edges than in the center, since there was a decrease in area of 24.37 per cent and in maximum depth of only 15.22 per cent. These changes caused an increase in mean slope of 19.31 per cent. Volume development increased by 18.18 per cent. Except for volume development between the original and the high-level stages, Sedge Point depression shows the same trends in morphometrical features (but to a less degree) that Bogardus Point depression did at corresponding stages. This is probably because both basins filled in the center faster than around the edges during the Algonquin stage and faster around the edges than in the center during the high-level and the present stages.

3. COMPARISON OF THE MORPHOMETRICAL CHANGES IN THE LAKE BASIN CONSIDERED AS A WHOLE

When Douglas Lake is considered as a whole, it is found that its area decreased 13.04 per cent from the Algonquin to the high-level stage and 7.7 per cent from the high-level to the present time. Maximum depth decreased little (3.98 per cent) from the Algonquin to the high-level stage because of the small amount of filling in Fairy Island depression (the deepest place), but maximum depth decreased 53.89 per cent during the high-level and the present stages because Fairy Island depression filled absolutely more than any other depression (104 feet). Mean depth decreased 40.19 per cent during the Algonquin stage and 36.59 per cent subsequently. The decrease in volume was 55.60 and 56.16 per cent; in mean slope, 36.86 and 24.44 per cent. Volume development decreased during the Algonquin stage 28.57 per cent but reversed this trend and increased in the subsequent stage by 20.00 per cent.

These morphometrical data indicate that during the Algonquin period the lake (as a whole) filled around the edges faster than in the deeper parts but filled in the depressions almost exclusively during the high-level and the present stages. Comparison of Figures 1, 2, and 3

(contour maps of the original, high-level, and present stages) and examination of Figures 4 (cross-section profiles) and 5 (graph of areas of contours) will make this generalization evident.

4. BOULDER BELTS

Boulders of considerable size (up to two feet in diameter) are found at several places around the edges of Douglas Lake. Some of them lie on deposits of sand many feet in depth. They were noted near borings 11, 21, 22, 38, 40, 49, 59, 71, 102, and 105 (Fig. 1). The texture of the material that makes up the shore in most localities mentioned is not such as to suggest that the shore is their source.

5. SAND STRATA IN DEPRESSIONS

Fairy Island depression had a layer of washed sand and gravel (up to 5 mm. in diameter) twenty feet in thickness at boring 2 and with an estimated thickness of thirty-five feet at boring 37, which lies between the marl of the warm-water deposit and the pink clay of the Algonquin (cold-water) deposit. Roberts Point depression had an eighteen-foot deposit of washed sand at boring 7 overlying the original bottom.

The depressions mentioned above accumulated very little deposit in their centers during the Algonquin stage and, consequently, their maximum depths were reduced only slightly. They are the basins that had the largest volumes as well as the steepest slopes at the end of the Algonquin stage. These findings make it seem likely that they were occupied longest by blocks of ice.

Volume of Sediment and Percentage of Filling of Basins

Table III shows the volumes of sediment of the various basins and the percentage of their filling. With the exception of Roberts Point and South Fish-Tail Bay depressions the absolute volumes of sediment that settled in the original depressions during the Algonquin stage of the lake (original to high-level in the table) were greater than those which accumulated subsequently (high-level to present in the table). The reverse is true, on a percentage basis, for all but Sedge Point depression. More than twice as much sediment settled in the lake as a whole during the first period as subsequently (4,582,776,000 and 2,058,089,000 cubic feet).

TABLE III

VOLUMES OF SEDIMENT (IN THOUSANDS OF CUBIC FEET) AND PERCENTAGE OF FILLING OF BASINS

Names of depressions	Original to high level		High level to present		Original to present	
	Volume of sediment	Percentage of basin filled	Volume of sediment	Percentage of basin filled	Volume of sediment	Percentage of basin filled
Fairy Island	836,101	57.08	546,560	77.07	1,465,188	90.00
Grapevine Point .	345,135	58.69	168,880	69.52	456,768	86.05
Maple Point	180,782	78.77	57,615	93.90	254,745	98.55
North Fish-Tail Bay	132,349	80.97	55,279	96.50	185,185	98.93
Bogardus Point ..	252,813	86.56	86,256	85.54	287,069	98.55
Roberts Point	128,816	30.00	184,432	61.35	152,915	56.77
South Fish-Tail Bay	24,945	12.92	115,119	54.73	121,836	56.13
Sedge Point	56,738	58.25	31,778	51.28	78,877	72.33
Stony Point	...	...	9,657	66.50	...	...
Boys Camp	112,248	100.00	...	...	...	...
Lake as a whole	4,582,776	47.99*	2,058,089	41.44*	6,640,865	69.54*

* Exclusive of that part of the basin above the present water level.

The average depth of sediment (Table II) that settled in the various depressions at the several periods shows the differences that have taken place in the rate of sedimentation. Considering the lake as a whole (exclusive of the basin lying above the present water level), the average depth of sediment that accumulated during the Algonquin period was 22.97 feet and that during the periods following, 11.86 feet. Conspicuous differences among the depressions occur between the Algonquin and the subsequent periods. For example, in Fairy Island depression an average of 30.30 feet settled in the first period and 60.30 feet afterward; for Bogardus Point depression the figures are 52.03 and 11.56 feet, respectively. The figures for the other basins range somewhere between these extremes.

Comparison of the average depths of sediment among the various depressions reveals striking differences for corresponding periods. For example, in Fairy Island depression during the high-level and the present periods 60.30 feet was deposited; in Grapevine Point depression, 24.84 feet; in Roberts Point depression, 15.50 feet; and in Sedge Point depression, 13.10 feet. These thicknesses are in great

contrast to those the writer found in the several depressions (much shallower) in Winona and Tippecanoe lakes in Indiana (Wilson, 1936, 1938), where the average depths of sediment were much the same.

Examination of the locations of the depressions in Douglas Lake (Fig. 2) shows that those in the most wind-exposed positions have the least average depth of sediment for the warm-water period; they are Sedge Point, Stony Point, and Roberts Point depressions. Fairy Island depression is in an exposed position and at the same time has the greatest average depth of sediment for the warm-water period (60.30 feet), but it lies at the lee end of the lake. It seems likely that swift currents over the wind-exposed basins do not give time for sediment to settle into them, whereas in Fairy Island depression less swift currents and the possibility that considerable quantities of sediment may be carried ultimately to that part of the lake by return currents could account for the great quantity of sediment that has settled there.

Discussion

The foregoing pages have described the diverse types of morphometrical changes that took place in the different depressions of Douglas Lake, the deposition of boulders over deep-sand deposits, the interpolation of sand and gravel layers between the Algonquin and subsequent deposits that occur in some depressions, and the thick deposits of pink clay (Algonquin deposits) around the margins of some depressions where there is scarcely any such deposit in the center. These phenomena can be adequately explained if it is assumed that the great ice blocks that occupied the depressions at the outset of the Algonquin period persisted for varying lengths of time in different depressions and did not disappear in Fairy Island depression until near the close of the Algonquin period. Such a theory implies that, where the ice blocks were thin, as they were around the margins of depressions, in the relatively shallow interdepression zones, and in shallow depressions, they melted early, and such localities became the first repositories of sediment and, therefore, accumulated the deepest deposits of cold-water sediment. Conversely, the deepest and most voluminous basins (at least in their centers) would be expected to become free of ice last and would accumulate the least deposit of cold-water sediment. It would be inferred that, after all

the glacial ice had melted, deposition of sediment would take place according to the distributive factors inherent in the lake as a whole and in the individual depressions.

These expectations are amply verified by the evidence. For example, it has been shown that during the Algonquin stage the very large Fairy Island depression filled almost exclusively around the margin, where the original block of ice was thin and undoubtedly melted early, whereas at the opposite extreme there stand Boys Camp and Bogardus Point depressions (that were originally shallow depressions), in which the ice melted early in the centers of the basins as well as around the edges and became filled almost entirely with pink-clay deposit. In South Fish-Tail Bay depression, which had very steep sides and was deep and well protected by Grapevine Point, its ice block apparently melted very little until late in the Algonquin period and, consequently, the depression has relatively little pink-clay deposit. The other depressions are intermediate between those already discussed.

That ridges on the original bottom of the lake began deposition early because they became free of ice seems well illustrated at boring 4, between Fairy Island and Roberts Point depressions. Here the original depth was only 42 feet (from the surface of the present basin), and there are only 25.5 feet of pink-clay deposit and one-half foot of recently deposited sandy organic matter. A similar example occurs at boring 8, in the interdepression zone, where there is a 42-foot pink-clay deposit that reaches to the base level of wave action and over which only one-half foot of sandy organic matter lies.

According to the general theory presented above, the boulder belts superimposed on sand could be explained by assuming that the sand deposits over which the boulders are lying were made around the margins of the depressions while the ice blocks in the centers of the depressions were anchored to the bottom. It may be assumed that during such a time wave action and currents were adjusting the shoreline and carrying sand into the water near shore. The melting block of ice may have contributed some sand to this zone. Finally, when the ice block in a depression freed itself from the bottom and floated, it may have drifted toward the shore and melted and thus have dropped its boulders on the previously deposited sand.

The presence of the sand and gravel layers interpolated between the cold- and warm-water deposits in the deepest depressions can

be explained in two ways: (1) One might assume that after the ice blocks had melted the increased wave action caused violent shore adjustments in which considerable sand was carried to the center of the depressions, where it settled before the deposition of warm-water sediment began; (2) The ice block could have dropped its burden of sand and gravel directly into the depressions as it melted, after it had become detached from the bottom and was floating.

The place of deposition of sediment during the Algonquin period was controlled to a large extent by the blocks of ice that occupied the depressions and, as has been shown, most of the sediment settled around the periphery of the depressions during that time. During the high-level and the present stages of the lake the controlling factors in distribution of sediment have been those inherent in the shape and form of the basin itself. In these later periods nearly all the sediment has settled in the centers of the depressions and very little around the periphery of the lake. This is what is to be expected in a lake as large as Douglas Lake, the long axis of which lies in the direction of the prevailing winds. That is, wave action is so vigorous that the shore out to the base level of wave action is being eroded and the abraded material is being carried away to settle in the depressions. Undertow and return currents down to the level of the thermocline and currents below that level at the spring and autumnal overturns probably keep the fine sediment suspended until it reaches the depressions, where it can settle to the bottom permanently.

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